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Largemouth Bass and Other Fishes in Ridge Lake, Illinois 1941-1963

orge W. Bennett
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This report is printed by authority of the State of Illinois, IRS Ch. 127, Par. 58.12. It is a contribution from the Section of Aquatic Biology of the Illinois Natural History Survey.

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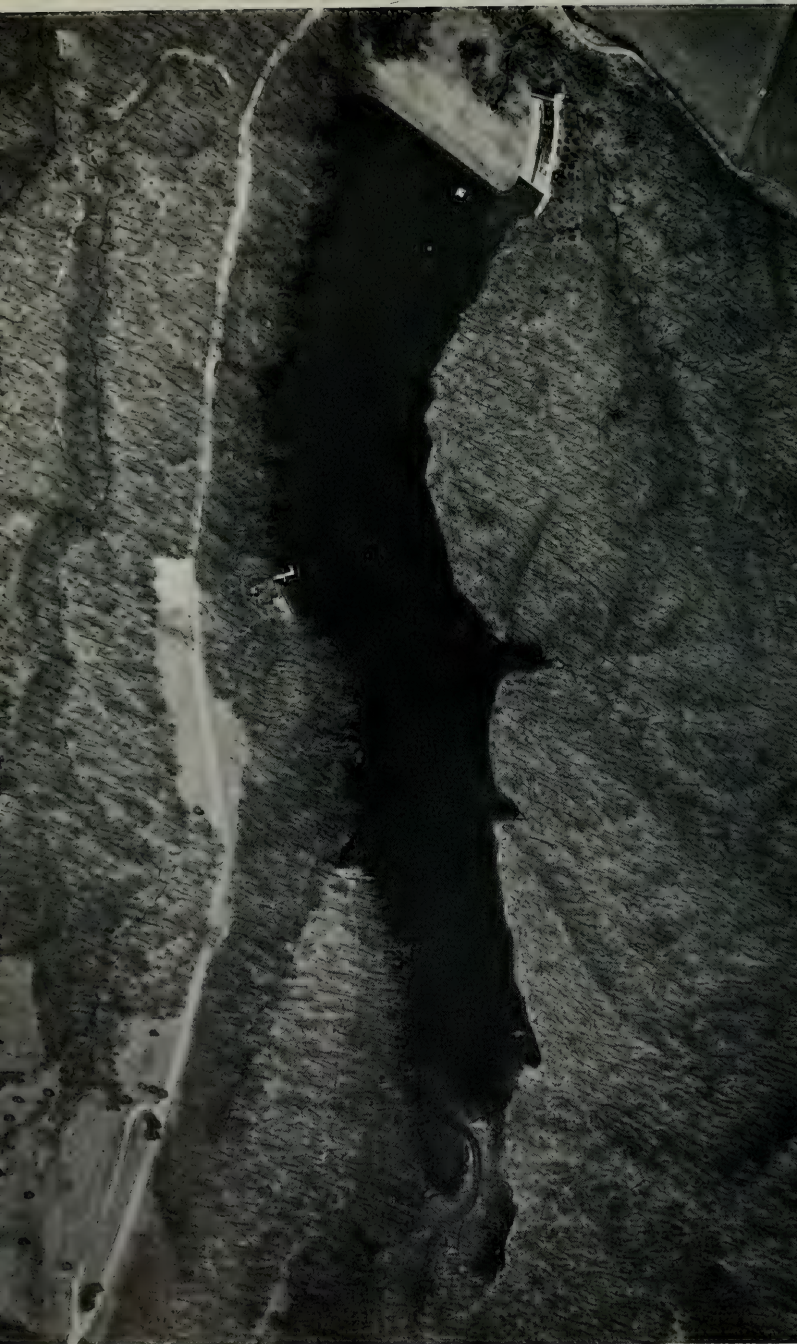

Largemouth Bass and Other Fishes in Ridge Lake, Illinois, 1941–1963

George W. Bennett
H. Wickliffe Adkins
William F. Childers

THE RESULTS OF STUDIES of fishes in the small artificial impoundment known as Ridge Lake (Frontispiece) in Fox Ridge State Park, Coles County, Illinois, have been presented in several publications. The first two were semipopular articles on the efficiency of various baits for largemouth bass, *Micropterus salmoides* (Lacépède), (Durham & Bennett 1949, 1951). Also in 1951 the same authors published an Illinois Natural History Survey Biological Note, *Cost of Bass Fishing at Ridge Lake, Coles County, Illinois,* in which they estimated that fishermen were spending approximately $1.22 per hour for travel, meals, equipment, and licenses to fish in the lake. When these average hourly costs were assigned to the average catch in pounds of bass per hour, the money spent to catch a pound of bass was calculated to be $8.66.

In 1954 the senior author prepared a bulletin entitled *Largemouth Bass in Ridge Lake, Coles County, Illinois* (Bennett 1954*a*) which covered the complete Ridge Lake investigation from its beginning in 1941 through a 10-year period of biennial drainings and censusings of the fishes. This report was followed by a preliminary one on "The Effects of a Late-Summer Drawdown on the Fish Population of Ridge Lake, Coles County, Illinois" (Bennett 1954*b*), describing the changes in the fish population resulting from two severe early September drawdowns by comparing it with the fish populations exposed in the five draining censuses of the previous 10 years.

Experiments with the Ridge Lake fish population have continued, and during the years since 1953 we have made additional studies of the effects of drawdowns, stable water levels, and the introduction of hybrid sunfishes. This report will carry these studies (in part) through 1963.

Ridge Lake has been of particular interest in experimental fish management because it can be drained completely and because it was built on a watershed somewhat larger than necessary or recommended on the basis of Illinois rainfall and runoff. Consequently, we know that when we drain the lake basin completely or partially in late fall or early spring, it will refill again in a minimum time. Since 1941 the lake has always refilled during the winter following fall drawdowns or drainings and has completely refilled following six spring drainings out of eight (between March and May). In those springs when it did not refill completely, the lake basin was more than half full by June.

This large watershed also has had its disadvantages in that the extent of soil erosion has been greater than it would have been in a smaller drainage basin. This factor and the fact that ravines above the lake are steep sided and the soil is light have made silting in the upper reservoir of sufficient magnitude to reduce the lake surface area by about 1 acre (0.4 hectare) in 10 years; that is, while the original surface area of the lake in 1941 was 18 acres (7.28 hectares), its area by 1951 had been reduced to 17 acres (6.88 hectares) and by 1963 to about 16 acres, or 6.48 hectares.

At this point it is evident that we are about to become involved in the confusion of English versus metric systems of measurements, and to give both English and metric measurements in a report of this length becomes redundant. Therefore, throughout this report the metric system will be followed. For those unfamiliar with or who have forgotten the English-metric equivalents, we are including them here.

Area:	1 hectare	2.471 acres
	1 acre	0.4047 hectare
Weight:	1 kilogram	2.205 pounds
	1 pound	453.6 grams or 0.4536 kilogram
Length:	1 meter	39.37 inches
	1 inch	25.4 millimeters or 2.54 centimeters
	1 kilometer	0.621 mile
	1 mile	1.609 kilometers

Pounds per acre may be converted to kilograms per hectare by multiplying the former by 1.121.

Kilograms per hectare may be converted to pounds per acre by multiplying by 0.892.

Some physical, chemical, and limnological characteristics of Ridge Lake have already been described (Bennett 1954*a*) and will not be repeated here except to restate that the growing season for fishes is 6–6½ months.

Under conditions of stable water levels Ridge Lake might be expected to support a mixed fish population of around 100,000 individuals larger than 65 mm total length, or 12,000–15,000 per hectare, weighing around 280 kg per hectare.

The lake shows intermediate "natural" fertility because the soil type in which it is built is less fertile than the black prairies of central Illinois and more fertile than the Ozark hills of southern Illinois. The fertility of the lake may have been increased somewhat over the past 23 years because of an influx of leaves and other organic matter from the surrounding hills and because nearly all flat lands in the Ridge Lake watershed are now rather intensively fertilized for increased production of corn and soybeans.

One of the more important aspects of the Ridge Lake study is that, because it is a long-term investigation, it demonstrates the variability of a fairly simple population of common fishes, not only in numbers and total weight, but also in the yield obtainable from angling. These variations are partly related to the application of various management techniques, but they are more importantly related to the incomplete ecosystem represented by the habitat and its plant and animal associations—incomplete because certain components are absent. This situation, we believe, is more or less the case with all artificial lakes and reservoirs and of many natural lakes.

ACKNOWLEDGMENTS

Nearly everyone who has been employed on the permanent or temporary staff of the Aquatic Biology Section of the Illinois Natural History Survey since 1941 has assisted in some capacity in the Ridge Lake investigation. In the early years Mr. Bruno von Limbach, Dr. Louis A. Krumholz, and Dr. Philip W. Smith contributed much time to general collections. On draining censuses the crew consisted of six to eight individuals and has included (in the order of the first census on which each worked) Dr. Donald F. Hansen, Mr. von Limbach, Dr. Krumholz, Mr. Jacob H. Lemm (deceased), Mr. Daniel Avery (deceased), Mr. Paul G. Barnickol, Dr. Arthur Witt, Jr., Dr. Leonard Durham, Dr. R. Weldon Larimore, Dr. William C. Starrett, Dr. James S. Jordan, Dr. William F. Childers, Dr. Robert C. Hiltibran, Mr. H. Wickliffe Adkins, Mr. Richard Ward, Mr. Howard Crum, Mr. Robert T. Crompton, Mr. Richard Bass, Mr. David McGinty, Mr. Ronald Havelka, and others. Also several members of the Illinois Department of Conservation have helped with one or several censuses: Mr. Sam A.

Parr (deceased), Mr. William J. Harth, Mr. Glee Fogelman (deceased), Mr. James Holmes (deceased), Mr. Quentin Pickering, Mr. George Kuhn (deceased), Mr. Ora Price, Mr. Bruce Muench, Mr. Arnold Fritz, and Mr. Rudy Stinauer.

As members of the Survey staff for varying periods, several persons gathered limnological samples and statistics on the anglers' catch: Mr. Robert G. Rennels, Dr. Smith, Mr. Vernon A. Anderson, Mr. Charles D. Kemp, Mr. W. W. Fleming, Dr. Morris Brehmer, and Mr. Adkins.

Mr. G. H. Boewe, Mr. Frank C. Bellrose, and Mr. Fleming made special studies of the flora of the lake. Dr. Witt and Dr. Durham studied the growth of Ridge Lake bass and bluegills from scale collections. The manuscript of this paper was read and criticized by Dr. Horace W. Norton, Professor of Statistical Design and Analysis, Department of Animal Science, University of Illinois, and it was edited by Mr. Robert M. Zewadski.

ORIGINAL STOCKING AND HISTORY

In 1963 the Ridge Lake experiment was in its 23rd year. In the spring of 1941 this newly completed 7.28-ha artificial impoundment was stocked with 435 largemouth bass, *Micropterus salmoides* (Lacépède), (Bennett 1954*a*: 236). These bass multiplied and their offspring have constituted the bass population of Ridge Lake during the entire period of its existence. More than 29,700 bass have been permanently removed from Ridge Lake by pole-and-line fishing and by Survey biologists during lake draining operations. The bass appeared to be as numerous in 1963 as in 1942. There was some evidence, however, that they were more difficult to catch in 1963–1968 than they were 25 years earlier.

Bluegills, *Lepomis macrochirus* Rafinesque, were first stocked in Ridge Lake in June and July 1944 when 129 were released (Bennett 1954*a*:236). These began to produce young almost at once, and it was estimated that more than 10,000 small ones were present when the lake was drained in the early spring of 1945. About 390,000 bluegills have been permanently removed from Ridge Lake through fishing and draining operations.

On the basis of the number of bluegills removed in 20 years as compared with the largemouth bass removed in 23 years, it was evident that the bluegills were much more prolific and/or capable of surviving than were the bass. When the lake was drained in the spring of 1949, we made a first attempt to remove the bluegills completely. However, enough bluegills gained entrance from outside sources or survived in the feeder stream, in spite of an attempt to poison them, to repopulate the lake with their next spawn.

In the spring of 1949, 138 warmouths, *Chaenobryttus gulosus* (Cuvier), were stocked in Ridge Lake. In contrast to the bluegill population, the number of warmouths has always remained small, and this fish has contributed very little to the hook-and-line yield.

Four stocks of channel catfish, *Ictalurus punctatus* (Rafinesque), have been released in Ridge Lake. Those released prior to 1963 were:

May 1, 1951, 675 fish 23–33 cm total length

November 5, 1952, 599 fish 13–46 cm total length

December 17, 1957, 473 fish 19–29 cm total length

The catfish were furnished by the Illinois Department of Conservation and were trapped in backwaters of the Mississippi River. Channel catfish grew well in Ridge Lake, and to fishermen they represented a "bonus" fish. They were never stocked in large enough numbers to contribute, in any 1 year, more than 20–30 percent of the total weight of the catch. One of these catfish grew to weigh 7.7 kg and several have weighed more than 4.5 kg; these large fish added to the general excitement of fishing at Ridge Lake by usually breaking lines when hooked.

In 1960, after an attempt was made to remove the bluegills by leaving the lake basin dry over the winter of 1959–1960 (Fig. 1), approximately 4,500 small hybrid sunfishes were stocked. This operation will be described in greater detail in a later section.

Also in 1960, 585 lake chubsuckers, *Erimyzon sucetta* (Lacépède), were stocked. Other fishes which found their way into Ridge Lake were green sunfish, *Lepomis cyanellus* Rafinesque; longear sunfish, *Lepomis megalotis* (Rafinesque); yellow bullheads, *Ictalurus natalis* (Lesueur); black bullheads, *Ictalurus melas* (Rafinesque); carp, *Cyprinus carpio* Linnaeus; black buffaloes, *Ictiobus niger* (Rafinesque); white suckers, *Catostomus commersoni* (Lacépède); and several species of stream minnows. The only members of this list which contributed to the fishermen's catch were green sunfish, yellow bullheads, black bullheads, and carp. All of these miscellaneous fishes were removed from the lake whenever found in draining censuses. These fishes probably moved into the lake from above as inhabitants of the Dry Run Creek watershed or were illegally stocked by persons unkown.

CREEL CENSUSES

From 1942 through 1963 (the end of the period covered by this report) Ridge Lake has been open to public fishing from eight Survey-owned boats during June, July, and August of each year except 1943. The lake was closed to fishing on Mondays and Tuesdays and open during the other 5 days of the week. Boats were furnished free and could be reserved in advance for the period from 6 to 10 AM or for 3 to 8 PM. When boats were not reserved, anyone could obtain permission to use them during the morning or afternoon periods.

Fishermen were checked out onto the lake in boats by the biologist at the laboratory pier and off the lake when they returned to record their catches and retrieve their state fishing licenses,

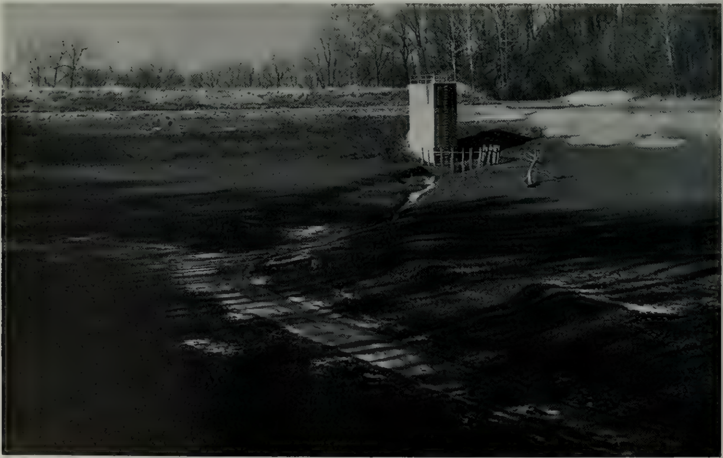

Fig. 1.— The dry basin of Ridge Lake during the winter of 1959–1960. The basin was allowed to dry completely and Dry Run Creek was permitted to run unimpeded through the lake basin to the Embarras River below the lake.

held by the biologist during each fishing period. Thus it was possible to collect information on the time spent in fishing; the catch in kinds, numbers, and weights; and the types of baits used. No restrictions were placed on baits, but if live minnows were brought to the lake, the biologist inspected them to forestall the escape of any carp, goldfish, or other undesirable species.

This method of taking a creel census gave a complete record of the time spent in fishing and the fishes caught. Signs on the lake dam and on the park roads warned that the lake was closed to fishing except from boats in this specific summer period, and it is believed that very little poaching took place.

DRAINING CENSUSES

A description of the method used in making a draining census at Ridge Lake was given in an earlier bulletin (Bennett 1954*a*:231–236). In the 1956 census a Wolf-type weir (Wolf 1951) built in the drain tunnel opening on the downstream side of the dam replaced the permanent vertical screen supported by concrete uprights and located about 15 meters below the outlet. The Wolf-type weir is an open-end box frame that is secured with its open end upstream in the lake outlet tunnel (Fig. 2). The sloping bottom of this frame as well as its sides are covered with 25-mm mesh hardware cloth, allowing a flow of water through its bottom as well as its sides. Water falls through the weir bottom by gravity. This arrangement is much more efficient in passing water than a vertical screen and much less likely to become clogged with leaves and debris.

Fishes entering the weir with the water were deposited on the sloping

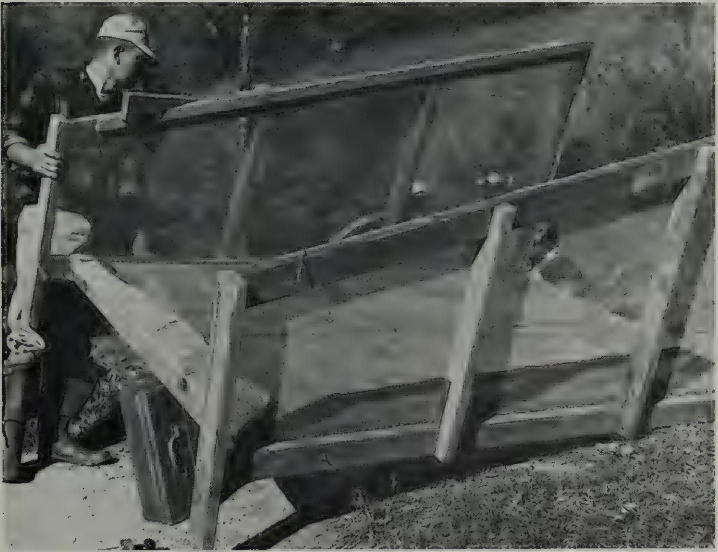

Fig. 2. — Body of the Wolf-type weir that fits in the outlet tunnel on the down stream side of the Ridge Lake dam. A wire mesh covered holding box (not shown) fits tightly against the open end of the weir (held by the biologist) and extends down into the water below while the weir is supported above the stream bottom. Water from the lake outlet enters the weir (at right) and falls through the mesh bottom of the weir, leaving the fishes to flop down the slope into the holding box.

hardware cloth bottom as the water passed through and they flopped down the sloping bottom into a submersed wire-mesh catch basin at the downstream end of the weir. The fact that the weir was in the outlet of the drain tunnel instead of in the stream channel some distance below eliminated the need to pump out pools and pockets in the stream channel between the outlet and the vertical screen to capture the last few fishes escaping from the lake.

Except for using the weir instead of the vertical screen, the draining censuses were all made in about the same manner. However, the census of 1959 was made in October, while all others were made in late March or early April. The fall of 1959 was a poor time to drain Ridge Lake because very little water was flowing in Dry Run Creek; consequently, many of the fishes that remained longest in the lake basin above the gate valve were forced to move about in an emulsion-like suspension of silt and water that tended to clog the fishes' gills and apparently had a high biological oxygen demand. This mud "soup" was quickly toxic to the fishes, and many died before we could get them into clean water. In spring draining operations a small stream of clean water was always flowing in Dry Run Creek, and fishes that collected in the lake basin immediately above the outlet were supplied with a source of clear, oxygenated water.

During all draining operations some very small fishes escaped being washed out of the lake with the water or being captured in the screen and censused by remaining in pools of Dry Run Creek above the dam. Later, when water was again impounded behind the dam, they moved down into the refilling basin where they were subjected to predation from the larger fishes put back after the census.

There is also a possibility that small numbers of fishes escaped from farm ponds in the Ridge Lake watershed in times of floods and passed down Dry Run Creek into Ridge Lake. These ponds may have been the source of the bluegills and warmouths that appeared in Ridge Lake in 1960 after the lake basin had remained dry during the fall and winter of 1959–1960. Such typical pond species as bluegills and warmouths, if washed from a pond into a stream, usually would move downstream in search of quiet water.

A work camp for processing the fishes was set up between the stilling basin and the lake outlet channel below the dam (Fig. 3). Fishes to be returned to Ridge Lake after a census were held alive in the water filled stilling basin of the surface spillway until the censusing was complete. Then, after a small volume of water had collected in the lake basin above the dam, the fishes were recaptured (Fig. 4), weighed, measured, "scaled" for age determinations, and returned to Ridge Lake.

All of the largemouth bass returned to the lake after a census bore fin clip marks (either the new mark of the current census or a mark of some previous census) prior to release; therefore, any unmarked bass taken in a fishing season following a spring census (except the current year-class spawned in the lake) were fish that had escaped being captured in the draining operation. Bluegills were not usually fin clipped, because even when censuses were made at 2-year intervals, the high mortality rate of bluegills assured that relatively few marked ones would be present at the next census.

The 25-mm mesh used in the fish screens and in the construction of the Wolf-type weir allowed small fishes to escape with the water as the lake was drained. No attempt was generally made to estimate the number of fishes that escaped through the mesh, but at certain censuses many more small fishes were present than at others. The census tabulations (unless otherwise specified) represent bluegills 64 mm or more in total length and largemouth bass 100 mm or more in total length.

During the first 10 years the lake was

drained completely and the fishes were censused at 2-year intervals (1943, 1945, 1947, 1949, and 1951) Following each census small fishes were culled. About half of the small bass were removed in the 1943 census, bass smaller than 25 cm total length were removed in the 1945 and 1947 censuses, bass smaller than 23 cm were removed in the 1949 census, and those smaller than 20 cm were re-

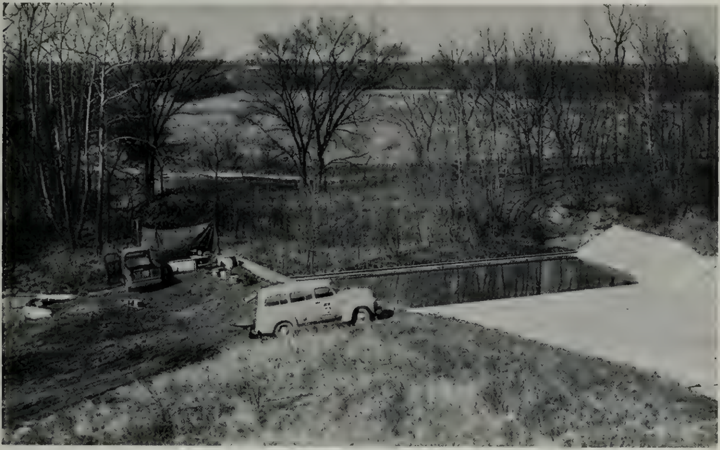

Fig. 3.— Fish censusing "camp" at the time of a spring draining census. Fishes to be replaced in the lake are stored in the water filled stilling basin (right) until enough water collects in the lake basin to allow the fishes to be returned.

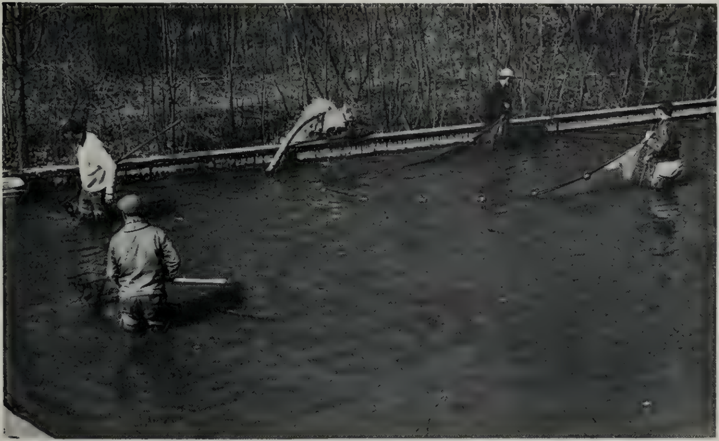

Fig. 4.— Recapturing fishes held in the stilling basin. When it is time to return the fishes stored in the stilling basin to the lake, the water is pumped from the basin and the fishes are recaptured with nets and short seines.

moved in the 1951 census. Bluegills were drastically culled at every census after they were introduced, and attempts were made to remove them completely in 1949 and 1959. The period 1941–1951 constituted the "Biennial Draining Period."

A period of testing September drawdowns of the lake level begain in 1951 and extended to the spring draining census of 1956, with an additional draining census in the spring of 1953.

A period of stable water levels when no management practices were applied to either the lake or the fish population extended from the spring of 1956 to October 1959 and included four complete fish growing seasons. The lake was drained completely in October 1959, the bass and catfish were removed to a nearby hatchery pond for winter storage, and the basin of Ridge Lake was allowed to dry for about 3 months.

In early 1960 Ridge Lake was allowed to refill, the bass and catfish were moved back from the hatchery pond, and hybrid sunfishes and lake chubsuckers were stocked from outside sources.

In the following pages we will consider the variations found in the fish populations supported by the lake at the times of the various censuses. Our major objectives are to consider the differences in the nine populations of fishes and the variability of the standing fish crops; to measure the negative relationships in numbers and weights between bass and bluegills; to consider reasons why Ridge Lake appears to have a maximum carrying capacity for largemouth bass; to reappraise the effects of early fall drawdowns upon the bass and bluegills of Ridge Lake; and to demonstrate the contrasting effects of stable and fluctuating water levels upon the fish populations of this lake.

STANDING CROPS OF FISHES

Table 1 shows the numbers and weights of largemouth bass, bluegills, and other fishes taken in the nine draining censuses of Ridge Lake. Bass numbered between 1,500 and 6,200, and their total weight varied between 205 and 412 kg. Bluegills numbered between 7,500 and 93,000 and weighed (exclu-

Table 1. — Numbers and weights of largemouth bass, bluegills, and other fish taken in nine draining censuses of Ridge Lake.

Census Year	*Largemouth Bass*		*Bluegills*		*Other Fishes*		*Totals*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
1943	4,771	393.4	0	. . .	36	4.1	4,807	397.5[a]
1945	1,641	323.3	10,061	57.6	762[b]	210.1[b]	12,464	591.0
1947	2,509	257.0	66,629	1,577.8	663[c]	257.7[c]	69,801	2,092.5
1949	2,039[d]	411.7[d]	19,714	709.4	110	23.6	21,863	1,144.8
1951	1,510	407.5	51,963	858.4	1,101[e]	70.8	54,574	1,336.7
1953[f]	1,964	204.8	7,476	449.1	937	247.1	10,377[f]	901.0[f]
1956[g]	2,242	289.3	17,180	924.6	886[h]	324.9[h]	20,308[g]	1,538.8[g]
1959[i]	2,354	240.0	92,669	1,246.5	2,289[j]	419.4[j]	97,312	1,905.9
1963	6,218	359.8	85,600[k]	1,051.4[k]	7,973[l]	445.6	99,791	1,856.8

[a] Only largemouth bass stocked; other fishes indigenous to Dry Run Creek watershed.

[b] These fishes were 544 black bullheads weighing 194.6 kg and 218 green sunfish weighing 15.5 kg.

[c] These fishes were 482 black bullheads weighing 73.9 kg, 56 carp weighing 176.8 kg, 1 black buffalo, and 124 green sunfish.

[d] Most satisfactory bass population from the standpoint of bass angling.

[e] These fishes were 916 warmouths, 159 black bullheads, 4 carp, and 22 minnows and small white suckers.

[f] This population was subjected to two 69-percent surface reduction drawdowns.

[g] This population was subjected to three 35-percent surface reduction drawdowns.

[h] These fishes were 622 warmouths weighing 35.3 kg, 237 channel catfish weighing 281.0 kg, and a few black bullheads.

[i] This census followed four growing seasons of stable water levels.

[j] These fishes were 172 channel catfish weighing 155.9 kg, 2,068 warmouths weighing 101.9 kg, 44 carp weighing 160.4 kg, and a few other miscellaneous fishes.

[k] Includes 72 hybrid sunfishes weighing 7.53 kg.

[l] Lake chubsuckers, warmouths, and channel catfish.

Table 2. — Numbers, total weights, and average weights of fish returned to or stocked in Ridge Lake following nine censuses.

Census Year	*Largemouth Bass*			*Bluegills*			*Warmouths*			*Channel Catfish*			*Lake Chubsuckers*		
	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams
1943	1,988	174.5	88	0	...	...	0	...	...	0	...	...	0	...	...
1945	647	233.9	362	61	11.6	190	0	...	...	0	...	...	0	...	...
1947	392	221.0	564	1,761	128.8	73	0	...	...	0	...	...	0	...	...
1949	1,027	365.0	355	0	...	...	0	...	...	0	...	...	0	...	...
1951	803	345.7	430	656	59.3	90	597	23.3	39	0	...	...	0	...	...
1953	604	166.1	275	1,477	127.8	86	173	24.4	141	601	194.0	323	0	...	...
1956	651	118.9	183	1,008	120.7	120	321	23.8	74	203	236.1	1,163	0	...	...
1960 (Fall 1959)	299	66.5	222	4,503[a]	121.6	27	0	...	...	41	36.9	900	585[b]	61.5	105
1963	2,386	203.2	85	4,492	122.5	27	1,335	29.4	22	11	44.8	4,073	1,020	110.4	108

[a] Bluegill x warmouth hybrids stocked after all bluegills were removed from lake; 448 red-ear x warmouth hybrids stocked in May 1961.
[b] Stocked from outside sources.

sive of the 1945 census when the bluegill population was just beginning to expand) from nearly 450 to about 1,580 kg. Before 1951 the other fishes were largely black bullheads, green sunfish, and carp, and from 1951 on, warmouths, channel catfish, carp, and lake chubsuckers. In three of the censuses, those of 1947, 1959, and 1963, the total population exceeded 1,800 kg in weight, but it varied from 398 kg when the population was almost entirely bass to 2,100 kg when the largest weight of bluegills was present.

In the two or more spawning and growing seasons between censuses, populations of bass, bluegills, green sunfish, warmouths, black bullheads, channel catfish, carp, and other species had an opportunity to expand. However, largemouth bass, channel catfish, and warmouths received greater consideration than bluegills, as most of the larger individuals were returned to the lake after the censuses. This was partly because these species were known to have low population expansion potentials (none at all for the channel catfish) and, in the case of largemouths, because we were particularly interested in managing bass as sport fish.

Actually, the reduction in the weight of largemouth bass put back after a census represented the removal of small fish and accidental losses of larger fish resulting from handling. The greatest reduction of bass occurred over the winter of 1959–1960 when the bass and channel catfish were held in a hatchery pond about 19 km from Ridge Lake. When these fishes were recaptured by draining the hatchery pond in the spring of 1960, the total weight of the bass found in the pond was reduced by 72.3 percent from the weight released there in October 1959.

Bluegills were severely reduced during each of the censuses. In no case were more than 4,500 of the larger bluegills put back after a census; usually the number returned was less than 2,000 (Table 2). Bluegills always showed great capacity for population expansion. As will be discussed later, the factors having a dampening effect on the rate of bluegill population expansion were

Table 3. — Numbers per hectare and weights per hectare of largemouth bass, bluegills, and other fish taken in nine draining censuses of Ridge Lake.

Census Year	*Largemouth Bass, Per Hectare*		*Bluegills, Per Hectare*		*Other Fish, Per Hectare*		*Totals, Per Hectare*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
1943	655	54.0	0	. . .	5	0.6	660	54.6[a]
1945	225	44.4	1,382	7.9	105[b]	28.8[b]	1,712	81.1
1947	345	35.3	9,152	216.7	91	35.4[c]	9,588	287.4
1949	280[d]	56.6[d]	2,708	97.4	15	3.2	3,003	157.2
1951	207	56.0	7,138	117.9	151	9.7	7,496	183.6
1953[e]	285	29.8	1,087	65.3	136	35.9[f]	1,508	131.0
1956[g]	326	42.0	2,497	134.4	129[h]	47.2[h]	2,952	223.7
1959[i]	342	34.9	13,469	181.2	333[j]	61.0[j]	14,144	277.0
1963	904	52.3	12,442[k]	152.8	1,159[l]	64.8[l]	14,504	269.9

[a] Only largemouth bass stocked; other fishes indigenous to Dry Run Creek watershed.
[b] These fishes were black bullheads, 75 per hectare averaging 0.356 kg each, and a few green sunfish.
[c] About 10 kg of black bullheads, almost 25 kg of carp per hectare, and a few other fishes.
[d] Most satisfactory bass population from the standpoint of bass angling.
[e] This population had been subjected to two 69-percent surface reduction drawdowns.
[f] Channel catfish, at 31.2 kg per hectare, and warmouths.
[g] This population had been subjected to three 35-percent surface reduction drawdowns.
[h] Mostly warmouths and channel catfish.
[i] After four growing seasons of stable water levels.
[j] Channel catfish, warmouths, and carp.
[k] Includes a few hybrid sunfishes.
[l] Lake chubsuckers, warmouths, and channel catfish.

Table 4.— Numbers per hectare and weights per hectare of largemouth bass, bluegills, warmouths, channel catfish, and lake chubsuckers returned to or stocked in Ridge Lake following nine censuses.

Census Year	*Largemouth Bass, Per Hectare*		*Bluegills, Per Hectare*		*Warmouths, Per Hectare*		*Channel Catfish, Per Hectare*		*Lake Chubsuckers, Per Hectare*		*Totals, Per Hectare*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
1943	273[a]	24.0	0	. . .	0	. . .	0	. . .	0	. . .	273	24.0
1945	89	32.1	8	1.6	0	. . .	0	. . .	0	. . .	97	33.7
1947	54	30.3	242	17.7	0	. . .	0	. . .	0	. . .	296	48.0
1949	141	50.1	0	. . .	0	. . .	0	. . .	0	. . .	141	50.1
1951	110	47.5	90	8.1	82	3.2	0	. . .	0	. . .	282	58.8
1953	88	24.1	215	18.6	25	3.5	87	28.2	0	. . .	415	74.4
1956	95	17.3	146	17.5	47	3.5	30	34.3	0	. . .	318	72.6
1959[b]	43	9.7	654[c]	17.7	0	. . .	6	5.4	85	9.0	788	41.8
1963	347	29.5	653	17.8	194	4.3	2	6.5	148	16.0	1,344	74.1

[a] Includes an estimated 65 small bass that escaped the 1943 census.

[b] Fall census; lake remained dry for 3 months and was restocked in spring of 1960.

[c] Bluegill x warmouth hybrids.

predation by large populations of largemouths and artificial drawdowns of the lake level.

Those who study fish populations may more easily visualize the fishes inhabiting ponds and lakes if numbers and weights are expressed in numbers and kilograms per hectare. For this reason we have included Table 3, giving the numbers and weights per hectare of the fishes found in the nine censuses, and Table 4, which gives the numbers and weights of fishes per hectare returned to the lake following each of the nine censuses.

The data shown in Table 3 indicated that the maximum weight of fishes that Ridge Lake would support in bass, bluegills, and such other fishes as have been present was around 280 kg per hectare (250 pounds per acre). This weight was exceeded slightly in the 1947 census, and the total weights of fishes were only slightly lower than that figure in the 1959 and 1963 censuses. In each of these censuses bluegills made up by far the greatest part of the fish population, both in numbers and weight.

Standing Crops of Largemouth Bass

When the populations of the species that were most abundant at Ridge Lake are considered as separate units, it may be conjectured that largemouth bass, bluegills, and warmouths have population maxima beyond which expansion is limited. For example, in the censuses of 1943, 1949, 1951, and 1963 the population of largemouth bass varied numerically between 207 and 904 fish per hectare although in each of these censuses the total bass weight was around 56 kg per hectare (54.0, 56.6, 56.0, 52.3). In the 1943 census the bass practically represented a one-species fish population for Ridge Lake, constituting 99 percent of both total number and total weight of all fishes (Table 5). At the other extreme when 904 bass per hectare were present (1963 census) and there was a large population of lake chubsuckers to produce young for bass forage, the total weight of bass was only 52.3 kg per hectare. At that time bass made up only 6 percent by number and 19 percent by weight of the entire fish population.

If the standing crop of fishes and the fish-carrying capacity of a body of water are related strictly to available food, we must assume that as much bass food was available when the entire population of the lake was composed of bass as was available when a variety of fishes was present. This may have been true, as Ridge Lake usually supports a large population of the crayfish, *Orconectes virilis* (Hagen), which is used extensively by largemouths.

In the censuses of 1945, 1947, 1956, and 1959 the total weight of bass supported by Ridge Lake ranged from 34.9 to nearly 45 kg per hectare (the 1953 census was excluded because its bass population was affected by the severe drawdowns). With the exception of the 1945 census when most of the fishes other than bass were bluegill fingerlings, these low weights per hectare of bass were associated with high weights per hectare of other kinds of fishes, suggesting competition between largemouth bass and certain other species.

Standing Crops of Bluegills

Bluegill numbers and total weights were lowest in seasons following the spring censuses because few were restocked (Table 4), and in the March census of 1945 after the initial stocking of 129 bluegills in June and July 1944. While the number of bluegills restocked after a census varied from none in 1949 and 1960 (in the latter year we attempted to replace bluegills with 654 bluegill x warmouth and red-ear x warmouth hybrids per hectare) to 653 per hectare in 1963, there was obviously no relationship between the number restocked and the number found in the census 2–4 years later.

For example, following the 1945 census, the rate of restocking was eight large bluegills per hectare, yet the weight

Table 5.— Percentages by species of total numbers and total weights of fish taken in nine draining censuses of Ridge Lake, with the total standing crops of fish.

Census Year	*Largemouth Bass*		*Bluegills*		*Warmouths*		*Catfish*		*Carp*		*Others*		Total Weight in Kilograms Per Hectare
	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight	
1943	99	99	0	0	0	0	0.5	0.8	0	0	0.5	0.2	54.6
1945	13	55	81	10	0	0	4	33	0	0	2	2	81.2
1947	4	12	95	75	0	0	1	3	tr[a]	9	tr	tr	287.4
1949	9	36	90	62	0	0	tr	2	0	0	tr	tr	157.2
1951	3	30	95	64	2	2	tr	2	tr	1	tr	tr	183.6
1953[b]	19	23	72	50	2	3	6	24	0	0	tr	tr	131.0
1956[c]	11	19	85	60	3	2	1	18	0	0	tr	tr	223.7
1959	2	13	95	65	2	5	tr	8	tr	8	tr	tr	277.0
1963	6	19	86	57	5	5	tr	3	0	0	3	16	269.9

[a] tr = Trace; less than 0.1 percent.

[b] Lake level lowered to reduce surface area from 6.88 to 2.12 ha in early September of 1951 and 1952 prior to spring draining of 1953.

[c] Lake level lowered to reduce surface area from 6.88 to 4.45 ha in early September of 1953, 1954, and 1955 prior to spring draining of 1956.

of bluegills per hectare in the 1947 census 2 years later exceeded that of any other year (Table 3). The 1959 census exposed 13,469 bluegills per hectare. This was the largest number in any census and appeared at the end of four growing seasons of stable water levels, suggesting that stable waters were favorable to the buildup of bluegill numbers. However, the number of bluegills produced over the three growing seasons of 1960, 1961, and 1962 and exposed in the March census of 1963 was almost as large (12,442 per hectare), and bluegills were not even supposed to be present in the lake.

In considering the populations of bluegills in the censuses after that of 1945 but excluding those of 1953 and 1956 (censuses following fall drawdowns), it was evident that there was much variation in the numbers and weights of these fish. Bluegills, unlike largemouth bass whose weights in four censuses were quite similar, achieved no weights similar enough to indicate a maximum standing crop figure for bluegills in Ridge Lake. The figure of 216.7 kg per hectare found in the 1947 census (Table 3) might suggest that the maximum carrying capacity for bluegills may be around 225 kg per hectare. There were no indications of relationships between the total weights of bluegills and of other fishes except largemouth bass. In years when largemouth bass weights per hectare were highest, bluegill weights per hectare were lowest, and vice versa. This relationship will be considered in more detail later.

Standing Crops of Warmouths

The warmouth is considered a very satisfactory pond fish (Larimore 1957). It was introduced into Ridge Lake in the summer of 1949 when 138 adult fish were released so that we could gain comparative information about the warmouth and the bluegill. Even though after each census warmouths were given a special restocking advantage over bluegills (much higher percentages of total populations were returned to the lake), warmouths never made up more than 5 percent of the total numbers and weights of all fishes in any census (Table 5). Total numbers of warmouths in the five censuses after 1949 were 916 in 1951, 252 in 1953, 622 in 1956, 2,068 in 1959, and 4,768 in 1963. Warmouths have contributed comparatively little to the Ridge Lake fish population.

BIENNIAL CULLING OF THE FISH POPULATION

During 1941–1951 Ridge Lake was drained and censused at 2-year intervals and only selected fishes were returned. This operation was described in detail in a previous publication (Bennett 1954*a*: 231–236) and will only be summarized here. The original stocking of the lake and the methods of operating creel censuses and making draining censuses have been described earlier.

Briefly, the culling procedure was to remove all bass smaller than 25 cm in the 1945 and 1947 censuses, 23 cm in the 1949 census, and 20 cm in the 1951 census (Table 6). In the 1943 census there were 4,771 bass between 15 and 20 cm. More than half of these fish were removed (2,783) to correct the overpopulation that had resulted in their stunting.

Nearly all of the bluegills were removed during each census, and the extent of these removals can be seen in Table 6. Removals of warmouths were relatively small in most censuses. The channel catfish removed were fish that were killed or injured in handling, as we tried to return as many of this species as possible. All other fishes except lake chubsuckers were completely removed from the lake during each census. These "other fishes" were largely bullheads, *I. melas* and *I. natalis;* green sunfish; and carp.

Small bass (less than 20 cm) and bluegills were culled as a final part of each census after the initial 10-year period. As may be seen in Table 6, the totals of fishes permanently removed from the

Table 6.—Numbers per hectare and weights per hectare of largemouth bass, bluegills, warmouths, channel catfish, and other fish permanently removed from Ridge Lake in draining operations, and totals for the entire lake, 1943–1963.

Census Year	*Largemouth Bass, Per Hectare*		*Bluegills, Per Hectare*		*Warmouths, Per Hectare*		*Channel Catfish, Per Hectare*		*Other Fish,*[a] *Per Hectare*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
Biennial Draining Period										
1943	382	30.0	0	. . .	0	. . .	0	. . .	5	0.6
1945	136[b]	12.3	1,374	6.3	0	. . .	0	. . .	105	28.8
1947	291[b]	5.0	8,910	199.0	0	. . .	0	. . .	91	35.4
1949	139[c]	6.4	2,708	97.4	0	. . .	0	. . .	15	3.2
1951	97[d]	8.5	7,048	109.8	44	1.2	0	. . .	25	5.3
Drawdown Period										
1953	198[d]	5.6	872	46.7	12	0.7	7	2.9	5	0.6
1956	231[d]	24.8	2,351	116.8	42	1.7	5	6.5	5	1.2
Stable Water Level Period										
1959	299[d]	25.2	12,815	163.5	215	7.5	20	17.3	7	21.8
Hybrid Sunfishes Period										
1963	557[d]	22.8	11,789[e]	135.0[e]	499	8.7	tr[f]	1.8	316[g]	27.6[g]
Totals for entire lake (not per hectare), 1943–1963	*16,451*[d]	*992.0*	*337,334*	*6,182.6*						

[a] Unless otherwise designated, these fishes consisted largely of black bullheads, green sunfish, and a few carp and miscellaneous minnows.
[b] Consisted almost entirely of largemouth bass of less than 25 cm.
[c] Consisted almost entirely of largemouth bass of less than 23 cm.
[d] Consisted almost entirely of largemouth bass of less than 20 cm.
[e] Included 72 hybrid sunfishes weighing 7.3 kg.
[f] tr = Trace; less than one fish per hectare.
[g] Included 2,162 lake chubsuckers and 10 golden shiners.

lake in the nine censuses were about 16,400 bass, 337,300 bluegills, and about 9,500 other fishes (totals not shown in Table 6). This culling operation increased the success of bass spawning (Table 10 and Bennett 1954*a*:246) because it removed many of the small bluegills and small bass that would have preyed upon bass fry and fingerlings of the new year-classes. It also increased the average growth rate of both bass and bluegills by reducing the numbers of smaller individuals of both species, which reduced the competition for food.

In a later section the effects of biennial culling on angling will be considered.

PERIOD OF ANNUAL FALL DRAWDOWNS

Drawdown studies were made during the 5 years from 1951 to 1956. This period may be subdivided into a 2-year period when severe fall drawdowns were made in 1951 and 1952 followed by a draining census in March 1953 and a 3-year period of less severe fall drawdowns in 1953, 1954, and 1955 followed by a draining census in March 1956. Results of the 1951–1953 severe drawdown studies have already been described (Bennett 1954*b*).

In brief, beginning in early September 1951 after the spring draining census and summer angling period, the lake level was lowered 4.6 meters in 96 hours by opening the drain outlet to allow the slow escape of lake water (Fig. 5). This release reduced the lake surface area from 6.88 ha to 2.12 ha and the maximum depth from 7.6 meters to 3.0 meters. The reduction in surface area amounted to 69 percent, and the reduction in total volume of water was considerably greater (Fig. 6).

All of the fishes and many of the larger aquatic invertebrates that inhabited the shallows of the lake were stranded on the exposed and drying bottom where they died, or if they moved down with the water, they were forced out of the debris and aquatic vegetation common to the shallow water and concentrated in water devoid of protective cover. In this open water the larger fishes could readily capture the smaller ones and the aquatic invertebrates. Thus, the numbers of small fishes and aquatic animals were rapidly reduced by being eaten by larger fishes or stranded.

The lake bottom was exposed to allow drying and oxidation of decaying organic materials. The drawdown level was maintained throughout September and October through the release of additional water when runoff from the watershed raised the level of the lake. Once the water temperature dropped below 18° C. (64.4° F.) in late October, the lake was allowed to refill. A similar program of water release was followed during the fall of 1952. In both years the lake had refilled by early March.

After the March draining census and the summer fishing period of 1953, a less severe September drawdown operation was begun. Instead of lowering the lake level 4.6 meters to give a lake surface area of 2.12 ha, the level was lowered only 3 meters to give a surface area of about 4.5 ha. This was a surface reduction of about 35 percent. After 3-meter fall drawdowns were made in 1953, 1954, and 1955, the lake was completely drained and censused in the spring of 1956.

The effects of the drawdown periods on the fish population of Ridge Lake may be seen in Tables 1 and 3. The total weight of fishes in the 1953 census (131 kg per hectare) was 26 kg per hectare less than in the lowest of the seven censuses, 1947 on, in which substantial populations of both largemouth bass and bluegills were present. However, when the fish population was figured on the basis of a 2.12-ha lake (resulting from the severe drawdowns of 1951 and 1952), the total weight of the fishes was considerably larger than 280 kg per hectare (630 kg per hectare). Evidently the downward adjustment of the weight of fishes to conform to the new lake area was only partly attained during the fall warm weather period when such adjustment might be expected to take place.

As suggested above, the effects of the drawdowns should be felt more among the small fish than among the large ones although actual stranding of fish by the receding water would depend to some extent on the behavior of individual species. Those species that normally frequent open waters away from the shore would be less likely to be trapped than would the species that use the plant growth and debris of shallow water for protection. Because small bass are more prone to move about in open water and bluegills tend to hide themselves among aquatic vegetation, there is a definite selection against the survival of small bluegills. On the other hand, open-water fishes (bass in this case) may become trapped in pools on an uneven lake bottom when the water level drops and leaves large pools that may be as much as 30 cm deep and 0.1 ha or more in extent. Of course, if these pools dry up before being reflooded, the trapped fishes of all kinds and sizes are lost.

The effects of the severe drawdowns of 1951 and 1952 were evident in the census of 1953. The weight of the bass population, 29.8 kg per hectare, was about one-half of the theoretical bass carrying capacity for the full lake, and as the number of bass in the 1953 census was comparable to the bass populations of other censuses, it may be assumed that there were fewer large bass than in most years (Table 3). This point will be considered in a later section when size distributions of these populations are discussed.

The most striking effects of the drawdowns were in the number of bluegills in the 1953 census as compared with bluegill numbers found in nondraw-

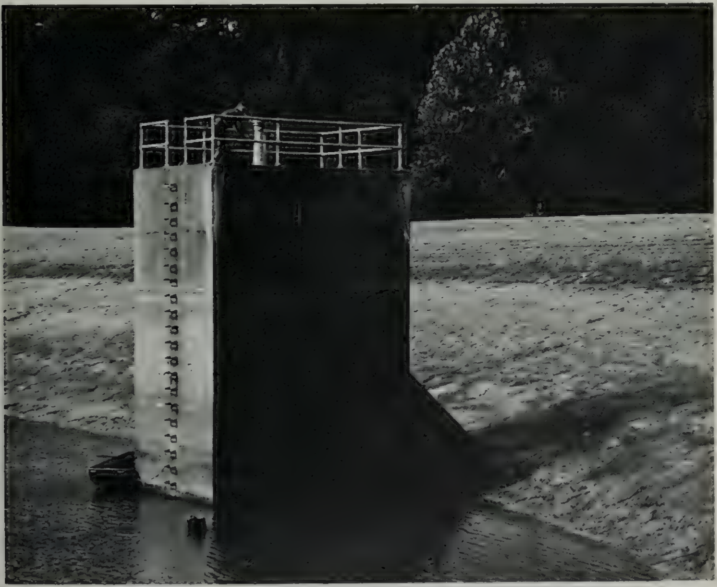

Fig. 5. — The outlet gate at Ridge Lake being opened by a hand-cranked jack on top of the outlet tower. In this photograph the lake level has been lowered about 4 meters. The ladder steps on the tower are approximately 30.5 cm (1 foot) apart.

down censuses and the sizes of the bluegills that survived. Only about 7,500 bluegills were taken, or 1,087 per hectare. The bluegill population found in other censuses ranged approximately from 2,500 to 13,500 per hectare. Still more striking was the fact that of the 7,500 bluegills that were present, more than half were of desirable sizes for angling (15 cm or larger) (Table 9), and those that were less than 15 cm total length were mostly within the 12.5–15 cm range. Other fishes in the 1953 census were warmouths and channel catfish. The drawdown may have improved the average size of the warmouths; it had no measurable effect on the channel catfish.

Three consecutive fall drawdowns of comparatively less severity (as described above) did not reduce the total weight of the Ridge Lake fish population beyond the range of variation of the nondrawdown censuses. Excluding the two censuses prior to the bluegill expansion of 1946, the standing crop of 223.7 kg per hectare found in the postdrawdown census of 1956 (Table 3) was exceeded in only three censuses and was greater in total weight than was found in three censuses.

Numbers and weights of largemouth bass were within the range of the other censuses. The 326 bass per hectare weighing 42.0 kg per hectare of the 1956 census were a more desirable bass population for angling than that of 1947 with 345 bass weighing 35.3 kg per hectare or that of 1959 with 342 bass weighing 34.9 kg per hectare.

Again in 1956 the bluegills showed the effects of the drawdowns. The total bluegill population numbered only about 17,200 (2,497 per hectare), about 2,500 less than the number in the census of 1949, the smallest nondrawdown census population of bluegills (19,700, or 2,708 per hectare). In most other censuses the numbers of bluegills ranged from slightly more than 50,000 to nearly 93,000 (or 7,000–13,500 per hectare).

Also in the 1956 census the number of bluegills 15 cm and larger exceeded those of less than 15 cm total length. As will be described in a later section, a larger total number of bluegills of desirable sizes was found in 1956 than was found in any other census, including

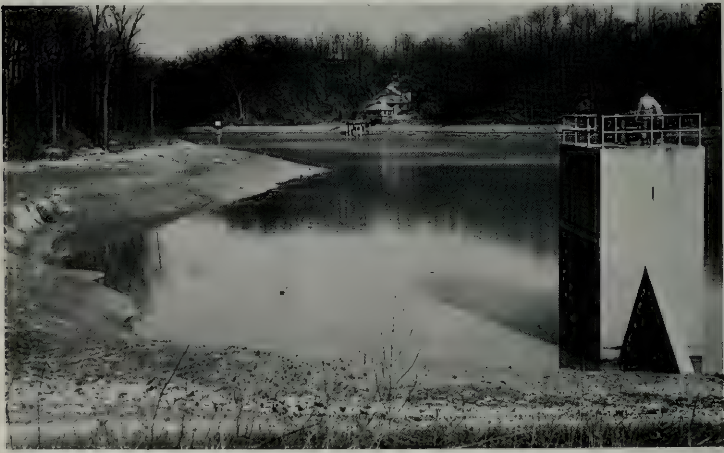

Fig. 6. — Ridge Lake, showing the outlet tower and laboratory after a 4-meter drawdown. Although not visible here, the lake basin is dry from a point opposite the laboratory to the upper end.

those of 1947 and 1959 in which the total bluegill populations numbered 66,600 and 92,700, respectively.

Again in 1956 other fishes consisted of warmouths and channel catfish and a few black bullheads. The warmouths appeared to benefit from the drawdowns, for during the drawdown period their average size was larger than in other periods. The channel catfish were also larger, but no cause could be assigned.

STABLE WATER PERIOD

Prior to the drawdown periods, 1951–1953 and 1953–1956, Ridge Lake had been drained, the fish population had been censused, and the lake had been restocked at 2-year intervals. The fishes that were held alive during each census to be replaced in the lake were rather severely culled. Population shifts observed at these 2-year intervals prior to 1951 gave only minor indications of what changes might take place in the relative abundance of the several kinds of fishes in the population if the lake were left alone for a longer period. Thus, it seemed worthwhile to leave Ridge Lake without draining censuses or drawdowns for at least four growing seasons.

The period of stable or nearly stable water levels began when Ridge Lake refilled in April after the draining census of March 1956 and continued until the draining census of October 12–16, 1959. This period included four growing seasons for fishes at Ridge Lake (Bennett 1954*a*:227; Markus 1932). During the four summers, 1956–1959, Ridge Lake was open to fishing as usual. The water level of the lake in this period varied from tower spillway crest level to a minimum of about 0.75 meter below the crest of the tower spillway. These fluctuations were believed to have had little influence on the fish population because they were "natural" fluctuations and because they made only a relatively small change in the area of the lake.

Tables 1 and 3 show that a numerically large population of bluegills developed in the 4-year stable water period, although the total number of all fishes was not as great as was found in the 1963 census, and the total weight of all fishes was less than was observed in the 1947 census.

The largemouth bass segment of the population appeared to be decreasing in weight although this point could not be verified statistically. The total number of bass, 2,354, or 342 per hectare, was intermediate and about the same as was found in the censuses of 1947 and 1956; the total weight of bass, 240.0 kg, or 34.9 kg per hectare, was the lowest of all nondrawdown censuses although that of 1947 was only slightly higher (Table 3).

In contrast to the bass, the bluegill population had increased to the numerical maximum found in any census, 92,700, or 13,469 per hectare. The total weight per hectare of the bluegill population, 181.2 kg, was exceeded only by that found in the 1947 census of 216.7 kg per hectare.

It is perhaps unfortunate that this fish population was not allowed to continue without a draining inventory for 2 or more additional years, as it appeared to be heading in the direction of reduced numbers of largemouth bass and overpopulation and stunting of bluegills. As will be shown in a later section, a large number of bluegills were caught by anglers during this period although after 1956 their average size was small.

COMPETITION: HYBRID SUNFISHES VERSUS BLUEGILLS

In 1960 we wished to begin testing the usefulness of two types of hybrid sunfishes in a location where we could obtain a complete creel census and check fishermen's minnow buckets for sunfishes that might contaminate a hybrid sunfish population. We chose Ridge Lake as the test site, and to prevent contaminating the hybrid population, we wished to remove all bluegills from the lake. An unsuccessful attempt to remove bluegills by poisoning the water after the 1949 census made it almost a certainty that they could not be successfully eliminated by rotenone treatment if such treatment were attempted in March (water temperature about 5° C.). Greater certainty of their elimination was expected if the lake were drained in October when Dry Run Creek was dry except when heavy rains gave temporary flow. Then if the gate valve in the Ridge Lake dam were left open over the winter so that no water would be left standing in the lake basin, any bluegills that survived anywhere in the watershed or lake basin would have a great opportunity to move downstream during periods of high runoff, finally arriving at the Embarras River several kilometers below the lake.

The lake was drained and censused October 12–15, 1959, and the largemouth bass and channel catfish to be restocked were stored in a state fish hatchery pond for the winter. The bass were saved so that we might retain the original strain that had been stocked in Ridge Lake 18 years before. The only reason for retaining the catfish was that they were of catchable sizes.

In all, 321 large bass weighing 161 kg and 200 small ones weighing 8.2 kg were placed in the hatchery pond along with 172 channel catfish weighing 156 kg. When the pond was drained in the spring it contained only 299 bass weighing 66.5 kg and 41 channel catfish weighing 36.9 kg (Table 2). It is quite possible that the missing bass and catfish were injured in handling or died from adverse conditions under the ice although there was no evidence of a general winterkill in the pond. All of the bass and catfish appeared emaciated when the pond was drained and many showed skin lesions that resembled furunculosis. In spite of their poor condition the 299 bass and 41 catfish were released in Ridge Lake in April 1960.

Bluegill x warmouth hybrids from a 1-ha nursery pond were moved to Ridge Lake during April 1960. These 4,503 fish ranged in length from 6.5 to 12.5 cm and weighed about 35 per kg. At the same period 585 lake chubsuckers were captured at a limestone quarry near Fairmount, Ill., and moved to Ridge Lake. In 1961, 448 red-ear x warmouth hybrid sunfish were added. These were also in the 6.5–12.5 cm range.

The experiment with the hybrid sunfishes was not a success because bluegills gained entrance to Ridge Lake and multiplied to compete with the hybrids. Also the hybrids were too easily caught by hook and line. As we had a 17.5-cm minimum length for taking these hybrids, a large number were captured and thrown back, many of which may have sustained injuries that later caused their deaths.

The creel record for 1960–1962 was the lowest of any period and was believed to reflect the interaction of the several factors mentioned above. The draining census of 1963 showed that the bass and the small number of remaining channel catfish had recovered from the effects of wintering in the hatchery pond. The lake chubsuckers had expanded their population to 3,200 from the original stocking of 585.

SIZE DISTRIBUTION OF LARGEMOUTH BASS AND BLUEGILLS

When a fish population is exposed in total, as occurs during a draining census, one has an opportunity to appraise the size distribution of the various species making up the population. The total number and the length distribution of a single species reflect its ability to compete with the other fish species present. The length frequency distribution also reflects the success of the individual year-classes constituting the life span of the fish species that is in review.

Angling demands maximum numbers of fishes of suitable sizes for sport and table use. It seems to matter not at all that these two criteria are antagonistic; that is, as the numerical size of a population increases, less food is available for each individual fish with the result that the opportunities for fishes to grow

Table 7.— Numbers and total weights of designated length-weight groups of largemouth bass taken in nine draining censuses of Ridge Lake.

Census Year	*Length Range*											
	12.7–24.9 cm		25.0–31.6 cm		31.7–36.7 cm		36.8–41.7 cm		41.8–46.9 cm		47.0–58.4 cm	
	Weight Range											
	0.068–0.222 kg		0.223–0.450 kg		0.451–0.903 kg		0.904–1.356 kg		1.357–1.810 kg		1.811–2.082 kg	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
Biennial Draining Period												
1943	4,754	368.4	0	. . .	0	. . .	2	2.1	15	22.9	0	. . .
1945	930	64.9	691	236.5	10	4.8	1	0.9	3	4.3	6	11.9
1947	2,105	39.8	233	77.0	87	45.9	34	33.6	49	57.7	1	3.0
1949	1,666	147.7	165	48.1	68	40.8	74	67.8	40	56.3	26	51.0
1951	948	79.3	270	77.6	108	58.6	157	146.5	14	18.7	13	26.8
Drawdown Period												
1953	1,823	96.6	61	13.8	5	3.3	37	32.9	28	37.5	10	20.7
1956	1,982	163.7	204	47.9	12	5.6	7	6.6	23	31.4	14	34.1
Stable Water Level Period												
1959	2,230	101.9	29	11.0	36	20.2	7	6.8	12	16.8	40	83.3
Hybrid Sunfishes Period												
1963	6,042	109.9	4	1.2	16	10.5	43	44.0	89	135.1	24	59.1

rapidly to desirable sizes are decreased. The reverse is also true; smaller numbers of fishes are usually associated with more rapid growth rates and larger sizes except in a few situations where the growth of certain pelagic fishes seems to be unrelated to the density of a population.

Where growth rates and large average sizes of fishes are density dependent, fish management must be a compromise. Maximum population numbers must be sacrificed in part to maintain a rate of growth that will produce fishes of catchable sizes; maximum growth rates and the development of fishes of maximum sizes must be sacrificed in part for the production of suitable numbers for reasonably successful angling. Often it is impossible to apply management at the same efficiency level to several species of fishes inhabiting the same water that one might apply if he were interested in one species to the exclusion of others. In a simple two-species combination such as the bass-bluegill, one might effectively manage for bass production and disregard the bluegills or manage for bluegills and disregard maximum production of bass. While the production of fishes for angling can be materially improved in either direction, it may be difficult or impossible to attain the maximum for both species at the same time.

In the Ridge Lake studies several management techniques were applied. Analyses of the size distribution and hook-and-line yields of the fishes should indicate the effectiveness of the techniques in question. These analyses will be presented in the following sections. A consideration of size distribution will come first.

Largemouth Bass

The size distribution of largemouth bass found in the nine censuses of Ridge Lake is shown in Tables 7 and 8. Table 7 gives the numbers and weights of largemouths divided into six length-weight categories. If we consider the numbers and total weights of fish in the four length categories from 25.0 cm to 46.9 cm, inclusive, it is quite evident that with the exception of 1943, the

Table 8. — Numbers and weights of largemouth bass of small and large sizes found in nine draining censuses of Ridge Lake.

Census Year	*Small (12.7–24.9 cm)*			*Large (25.0–58.4 cm)*			*Totals*	
	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Weight in Kilograms
				Biennial Draining Period				
1943	4,754	368.4	77.5	17[a]	25.0	1,470.6	4,771	393.4
1945	930	64.9	69.8	711	258.4	363.4	1,641	323.3
1947	2,105	39.8	18.9	404	217.2	537.6	2,509	257.0
1949	1,666	147.7	88.7	373	264.0	708.0	2,039	411.7
1951	948	79.3	83.6	562	328.2	584.0	1,510	407.5
				Drawdown Period				
1953	1,823	96.6	53.0	141	108.2	767.4	1,964	204.8
1956	1,982	163.7	82.6	260	125.6	483.1	2,242	289.3
				Stable Water Level Period				
1959	2,230	101.9	45.7	124	138.1	1,113.7	2,354	240.0
				Hybrid Sunfishes Period				
1963	6,042	109.9	18.2	176	249.9	1,419.9	6,218	359.8

[a] Survivors of the original bass stocking of 1941.

Table 9. — Numbers, total weights, and average weights of bluegills in three length classes taken in nine censuses of Ridge Lake, and the total numbers and weights of all bluegills in each of the censuses.

Census Year	*Small* (6.4–14.9 cm)			*Minimum Useful Sizes* (15.0–19.9 cm)			*Large Useful Sizes* (20.0–25.1 cm)			*Totals*	
	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Weight in Kilograms
				Biennial Draining Period							
1943	0	. . .	. . .	0	. . .	. . .	0	. . .	. . .	0	. . .
1945	10,000[a]	46.0[a]	5	0	. . .	. . .	61	11.6	190	10,061	57.6
1947	59,754	1,076.5	18	6,873	500.9	73	2	0.4	200	66,629	1,577.8
1949	16,625	418.8	25	3,089	290.6	94	0	. . .	. . .	19,714	709.4
1951	51,300	798.3	16	663	60.1	91	0	. . .	. . .	51,963	858.4
				Drawdown Period							
1953	3,057	103.8	34	4,383	338.5	77	36	6.8	189	7,476	449.1
1956	8,519	207.7	24	8,620	709.2	82	41	7.7	188	17,180	924.6
				Stable Water Level Period							
1959	88,200	842.9	10	4,469	403.6	90	0	. . .	. . .	92,669	1,246.5
				Hybrid Sunfishes Period							
1963	85,524	1,043.6	12	4	0.27	68	0	. . .	. . .	85,528	1,043.9

[a] Estimated.

largest numbers and weights of bass were found in the period of biennial draining, 1941–1951.

Table 8 shows a simplified breakdown of large and small bass taken in the nine censuses. In each census during the first 10 years except that of 1943 when an overpopulation of small bass resulted from the 1941 spawn, the total number and weight of bass 25 cm or longer were more than 370 weighing 215 kg or more. In none of the censuses after 1951 did the number of large bass approach 370 and only in the 1963 census was the total weight of large bass more than 215 kg. Thus, the censuses during the biennial draining period, 1941–1951, indicate the usefulness of this technique in building up populations of large bass. The relatively high weight of large bass in the 1963 census was chiefly due to the presence of 89 bass in the 1.4–1.8 kg category, which, as will be shown later, were nearly immune to capture by angling.

Bluegills

The total numbers, total weights, and average weights in three length classes of bluegills are shown in Table 9. The first census when numbers of bluegills were available was in 1947, and they have since continued to be present in substantial populations.

The largest numbers of bluegills 6.4 cm and longer were present in 1947, 1951, 1959, and 1963, but the best potential populations for angling were present in the census of 1947, 1953, 1956, and 1959.

By far the largest population of bluegills of useful sizes was exposed in the 1956 census after three consecutive seasons of mild early fall drawdowns. The 8,661 large bluegills (15 cm and over) weighing about 715 kg were about one-third larger in numbers than the next best population (that of 1947) and about two or more times as large in numbers of large bluegills as most other populations. Even following 2 years of severe fall drawdowns the 4,419 large bluegills in the 1953 census were numerically almost equal to the 4,469 large bluegills of the 1959 census after four seasons of stable water levels. Here is evidence of the importance of drawdowns in bluegill management.

Bluegills of 20 cm or more total length were found in the censuses of 1945 and 1947 (survivors of the original stocking of 1944) and in the censuses of 1953 and 1956 during the period of drawdowns. In contrast, neither the biennial culling technique nor the periods of stable water levels, 1956–1959 and 1960–1963, produced *any* bluegills as long as 20 cm.

BASS SPAWN INVENTORY

The idea of making an annual inventory of the schools of bass fry originated on May 29, 1941, when the first schools of young spawned by the original stock were in evidence along the lake shallows (Bennett 1954*a*:245). Between May 30 and June 7, 1941, we made daily counts of these schools of fry. The number of schools gradually increased until 38 were counted on June 5. After that date the number of schools decreased, and bass fry from schools that had broken up were scattered along the lake edges in the shallow water over the shore ledge (formed by wave action) where the slope of the natural bank was steep. The estimate of bass fry in the 38 schools was 76,000, or nearly 21,000 per hectare on the basis of the 3.64-ha surface area of the lake at that time. This estimate indicates an average of 2,000 fry per school. Our estimate was probably conservative, but it was not considered desirable or possible to capture an entire school and count the fry. Rough counts were made by estimating the numbers of fry in groups of 100, and it was seldom that a school was estimated at more than 3,000 fish; usually they appeared to number 2,000 or less. However, in 1951 a huge school was located around the concrete spillway tower that was estimated at 10,000 fry and probably contained more. This school was found around three sides of the tower, a linear distance of 10 meters; extended about 2.5 meters out from the tower; and occupied at least 0.6 meter in depth.

Conditions for censusing bass fry varied from year to year. Turbid water and wave action sometimes reduced visibility. The schools of fry often moved under floating mats of algae (present in some years) and were difficult to locate. However, rooted vegetation growing on the bottom had not grown sufficiently by late May or early June to obscure the schools.

A maximum count of schools usually was recorded 3–6 days after the first school was located, and this maximum was considered the number of bass fry for each season. In Table 10 the fry estimates are given in terms of numbers per hectare. While the numbers estimated are in no way meaningful as such, the fact that we followed similar methods using identical personnel from year to year has led us to believe that these counts have comparative value.

In some years no schools of fry could be found. This did not mean that none were present; rather it probably meant that the number of schools was so small that we were unable to find them or that predation by yearling fishes took place so rapidly that the schools were decimated before the individual fry progressed much beyond the free-swimming stage.

The fact that large numbers of fry were found in a given year did not necessarily mean that a large year-class of bass would develop from them. As we shall see in the following section, there were large differences in survival rates from year to year, and it was impossible to predict survival for any given year.

The bass fry estimates given in Table 10 have been separated into three groups on the basis of management operations that we believe may have influenced bass fry numbers. The greatest numbers of fry were associated with biennial lake draining and culling operations. These operations removed almost all of the small yearling fishes that would feed upon bass eggs and fry, reduced numbers of large crayfish that might disturb bass nests, and probably also reduced predacious insect larvae which are known to attack fry. The average number of fry associated with the culling operations in nine draining censuses was 7,917 per hectare.

Fall drawdowns of Ridge Lake were believed to have similar but less severe effects upon the small fishes, crayfish, and other aquatic invertebrates. Here the data are less convincing because only 3 years were represented. Thus, the average number of young bass in the censuses associated with drawdowns (3,243 per hectare) suggested that such operations were only about 40 percent as efficient as draining and culling in promoting the successful production of bass fry.

There were 10 years when seasons of stable water levels without any type of population reduction preceded bass spawnings. With two exceptions the fry production or fry survival in those years was relatively small. The first exception was in 1942 when the fry count was 3,570 per hectare. At that time the population of Ridge Lake was composed almost entirely of bass, including a few of the original spawners and the 1941 year-class, fishes ranging in length from 18 to 28 cm. These bass were not interested in eating fishes of fry sizes.

In 1957 the bass fry estimate was 4,880 per hectare. Why the survival of fry to the schooling stage in this year was reasonably good is unknown. When the 2 exceptional years are included, the average number of fry in seasons following a year of stable water levels is 1,023 per hectare. If these 2 years had been omitted, the average would have been around 220 per hectare. Thus, the differences in the numbers of bass fry associated with two types of management as compared with the numbers of fry associated with no management appear to be very significant.

Several questions arise when large numbers of schooling bass fry are in

Table 10. — Estimated numbers of largemouth bass fry per hectare in seasons following culling operations for small bluegills and age classes 0+ and 1+ bass, 1 or more years of stable water levels, and 1 or more years of early fall drawdowns.

Spawning Seasons Following					
Biennial Draining and Culling		*Stable Water Levels*		*Fall Drawdowns*	
Year	Estimated Number of Fry Per Hectare	Year	Estimated Number of Fry Per Hectare	Year	Estimated Number of Fry Per Hectare
1941[a]	20,860[b]	1942	3,570	1952	5,010
1943[a]	2,470	1944	140	1954	2,760
1945	15,920	1946	340	1955	1,960
1947	5,080	1948	0[c]		
1949	5,390[d]	1950	0[c]		
1951	4,390	1957	4,880		
1953	10,460	1958	430		
1956	3,630	1959	580		
1960	3,050	1961	0[c]		
		1962	290		
Total	*71,250*		*10,230*		*9,730*
Average	*7,917*		*1,023*		*3,243*

[a] Fish population almost entirely largemouth bass.

[b] Calculations for year based on actual water level, giving a surface area of about 3.6 ha (Bennett 1954a:248).

[c] No schools of young bass were found.

[d] Estimate based on lake surface area of 4.4 ha (Bennett 1954*a*:231).

evidence: (i) Does this mark the beginning of a strong new year-class? (ii) What is the survival rate; that is, how many young from these schools will survive to become yearling bass and be found in the next draining census? (iii) How many sexually mature bass were present in the lake when this large spawn was produced? (iv) What was the composition and density of the fish population (bass and other fish) that allowed the substantial fry survival? In the following sections we have attempted to unravel some of these relationships.

SURVIVAL RATIOS OF BASS: FRY TO 2-YEAR-OLDS

In the period of biennial draining and culling, 1941–1951, the fish thinning operation associated with each lake draining was followed by a relatively successful spawn of bass in the next spawning season. This new year-class usually showed good (probably exceptional) survival of fry, at least to the free-swimming stage. As mentioned earlier, this survival was the result of the reduction in numbers of the fauna which normally might attack bass as embryos, yolk-sac fry, or schooling fry by the draining operation and the removal of small fishes of the 0+ age group.

After we had counted the schools and estimated the number of bass fry produced following each lake draining, we had the opportunity to count the numbers of 21-month-old bass, resulting from these fry, present in the succeeding draining census. If we added to the small 1+-year-old bass found in the draining censuses the small bass of the same age group taken by fishermen in the interim, we could set up a rough ratio of the number of bass fry required in a 2-year period to produce one bass of 0+ to 21 months of age.

Such a ratio would be affected by all mortality factors including angling. In Table 11 (from Bennett 1954*a*:251) we have listed the estimated numbers of bass fry per hectare, the 1+ bass caught

Table 11.—Estimated number of largemouth bass fry per hectare in each of five year-classes produced in Ridge Lake, the number of bass per hectare of each year-class either caught by fishermen in the next two fishing seasons after spawning or appearing in the next draining census about 21 months after spawning, and the ratio of fry to fish subsequently taken. These figures indicate survival of fry to become yearlings. Calculations involving water surface area were based on 7.28 ha except where stated otherwise.[a]

Year-Class	*Estimated Number of Fry Per Hectare*	*Number Per Hectare of Bass of Designated Year-Class Taken in the 21 Months After Spawning*			*Ratio of Fry to Subsequent Take*
		By Fishermen	In Draining Census	Total	
1941	20,860[b]	69	657[c]	726	29 to 1
1943	2,470	. .	62	62	40 to 1
1945	15,920	37	44	81	196 to 1
1947	5,080	42	126	168	30 to 1
1949[d]	5,390	49	111	160	34 to 1

[a] From Bennett (1954*a*:251).
[b] Calculations for this year based on actual water area of about 3.6 ha at spawning time.
[c] Figure includes an estimated 473 bass that escaped the 1943 census.
[d] Calculations for 1949 based on actual lake surface area of 4.4 ha during the summer.

by fishermen, and those found in the draining censuses. The ratios of fry to 1+ yearlings varied between 29 to 1 and 196 to 1. Because of the exceptional survival of bass fry following each culling, all of these ratios are probably abnormally low.

It is evident from the table that, in Ridge Lake at least, a large number of fry does not necessarily result in the formation of a strong new year-class. In 1941 a dominant year-class was formed when bass fry were numerous (20,860 per hectare), and the survival ratio was estimated to be approximately 29 to 1. In 1945 a strong year-class was not formed even though there were about 15,900 fry per hectare. Poor post-fry survival resulted in a ratio of almost 200 to 1 for the 2-year period.

RELATIONSHIPS BETWEEN BASS SPAWNERS, BASS FRY, AND TOTAL FISH POPULATION DENSITY

In each draining census we made an appraisal of the numbers of sexually mature bass, small immature bass, large and small bluegills, and other fishes. These components of the populations were compared with the estimated number of bass fry enumerated during the following spawning season in the 1941–1953 period when biennial population censuses were conducted. The results are shown in Table 12, in part from Bennett (1954*a*:248) and in part from new data.

It quickly became obvious that there was a negative relationship or no relationship between the number of spawners per hectare and the estimated numbers of bass fry produced. The largest numbers of fry were found in 1941, 1945, and 1953, and in those years the numbers of bass spawners in the lake were 27, 89, and 88 per hectare, respectively. In 1948, 96 bass spawners per hectare produced so few schooling fry that none were seen; in 1949, 176 bass spawners per hectare produced an estimated 5,390 fry per hectare.

More significant relationships were evident when we compared bass survival rates with the relative abundance of small bluegills. When 2,800 or more small bluegills were present per hectare, as in 1946, 1948, and 1950, bass fry survival was low. Prior to 1944 when no bluegills were present with the bass, the estimated number of young bass surviving to the fry stage was always

Table 12. — Estimated numbers of bass, bluegills, and other fish per hectare shortly prior to spawning time, and of largemouth bass fry at spawning time, 1941–1953, at Ridge Lake. Calculations involving water surface area were based on 7.28 ha before the 1951 fishing period and 6.88 ha from that time on.[a]

Year	*Largemouth Bass Per Hectare*		*Bluegills Per Hectare*		*Other Fish Per Hectare*		*All Fish Per Hectare*		*Estimated Bass Fry Per Hectare*
	25 cm or Longer	Less Than 25 cm	15 cm or Longer	Less Than 15 cm	Large	Small	Large	Small	
				Biennial Draining Period					
1941	27[b]	0	0	0	0	0	27	0	20,860
1942	69[c]	653	0	0	5	0	74	653	3,570
1943	2	271	0	0	0	0	2	271	2,470
1944	162	128	0	0	72	37	234	165	140
1945	89	0	8	0	0	0	97	0	15,920
1946	105	290	1,045	6,965	42	79	1,192	7,334	340
1947	54	0	242	0	0	0	296	0	5,080
1948	96	273	740	2,768	40	10	876	3,051	0
1949[d]	176	57[e]	0	0	0	0	233[f]	0	5,390
1950	105	173	144	7,117	49	138	298	7,428	0
1951	72	38[g]	90	0	6[h]	76[h]	168	114	4,390
				Drawdown Period					
1952	40	359	863	676	156	17	1,059	1,052	5,010
1953	88	0	215	0	112	0	415	0	10,460

[a] In part from Bennett (1954*a*:248).
[b] Calculations for 1941 based on actual water area of 3.6 ha at spawning time.
[c] Includes only 7 bass of spawning age per hectare.
[d] Calculations for 1949 based on actual water area of 4.4 ha during summer.
[e] None less than 23 cm.
[f] Small bass are included in the large-fish category here because they were all at least 23 cm and therefore were uninterested in fry-sized prey.
[g] None less than 20 cm.
[h] Warmouths only.

2,400 or more per hectare (Table 10). Estimated numbers of bass fry were large from 1951 to 1953, inclusive, probably because the numbers of small bluegills were held in check by the severe drawdowns of that period.

Table 12 was not carried beyond 1953 because there were no further 2-year intervals between drainings, and it was therefore impossible to estimate populations in a sequence of years such as was followed until 1953.

EXPANSION POTENTIAL OF BLUEGILLS IN RIDGE LAKE

As described in the introductory sections, bluegills showed great ability to expand their populations in Ridge Lake. This expansion was positively related to time (two, three, or four growing seasons) and negatively related to "dominant" bass populations and drawdowns. There seemed to be no relationship between numbers of large bluegills returned to the lake after a census and the numbers present in the next succeeding census 2, 3, or 4 years later.

Table 13 shows the numbers of bluegills restocked after seven censuses, including the census of 1945 after bluegills were originally stocked in 1944 and all later ones. These censuses are arranged in order of increasing numbers of bluegills returned, ranging from zero in 1949 and 1959 to 242 per hectare in 1947.

The fact that there appears to be no relationship between the number of bluegills restocked and the number present two, three, or four growing seasons later may relate to two phenomena: (i) the high reproductive potential and survival of bluegills in the lake and (ii) the fact that unknown numbers of very small bluegills may have survived the cen-

Table 13. — Number of bluegills restocked per hectare following a named census and number per hectare taken in the following census 2, 3, or 4 years later. Data are arranged in order of numbers of bluegills restocked.

Census Year	*Next Census Year*	*Growing Seasons Between Censuses*	*Bluegills Restocked Per Hectare Following Census (Col. 1)*			*Bluegills Per Hectare Present in Census Following Restocking (Col. 2)*		
			Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams
1949	1951	2	0	. . .	. . .	7,138	117.9	16
1959	1963	3	0[a]	. . .	. . .	12,442	152.8	12
1945	1947	2	8	1.6	200	9,152	216.7	24
1951	1953	2	90	8.1	90	1,087[b]	65.3	60
1956	1959 (Fall)	4	146	17.5	120	13,469	181.2	13
1953	1956	3	215	18.6	86	2,497[c]	134.4	54
1947	1949	2	242	17.7	73	2,708	97.4	36

[a] An unknown number of bluegills entered the lake from the watershed or an undetermined source.
[b] Subjected to 4.6-meter drawdown 1951 and 1952.
[c] Subjected to 3-meter drawdown 1953, 1954, and 1955.

suses by staying in Dry Run Creek pools until water again accumulated behind the dam. This escapement was evident in 1949 when the creek above and within the lake basin was treated with a strong dosage of rotenone. Obviously the treatment was unsuccessful, probably because the water temperature was below 13° C. and rotenone is fairly inefficient in cold water. Although no bluegills were restocked after the census, enough were present to expand to a population of 7,138 per hectare by 1951.

The two smallest bluegill populations were found in the censuses following drawdowns (1953 and 1956). Only slightly larger than the number found in 1956 was that found in 1949 which developed in a period when the bass population was at its weight peak (Table 3).

MORTALITY FACTORS AND LENGTH OF LIFE

Most species of fishes are relatively short lived even if they are entirely protected from predation or disease. In aquatic habitats away from human influences, mortality factors for fishes are so numerous that of the thousands of small fishes produced at a single spawning only a few survive to become adults. Most of this mortality takes place in the larval and post-larval stages when the fishes are very small. Fishes of large species that survive to the second growing season are subjected to predation from far fewer predators, and as the fishes become still larger, the predators are progressively fewer until the largest fishes may be preyed upon only by a few large mammals and birds.

Large fishes that survive to "old" age for their species may eventually become emaciated and die, perhaps because of their inability to capture sufficient food. The authors have seen a number of large bass that were emaciated to the point that they were "all head." One of these bass, which was 63.5 cm in total length and weighed 2.7 kg, would, if of average plumpness, have weighed 4.5–5.4 kg. There is some satisfaction in seeing fishermen catch these senile bass, because one can be certain that such fish would soon die of old age.

At Ridge Lake bass ages were determined by the presence of annuli on their scales and by fins clipped at the time of each draining census from fishes not previously so marked. Bass marked at a previous census were not re-marked but were weighed, measured, and "scaled," and the previous fin clip was recorded.

After each census a recorded number of marked bass bearing the fin clip of the current census or those of previous censuses were restocked in the lake to be caught by fishermen in the next two, three, or four fishing seasons or to appear as marked individuals in the next draining census.

In eight draining censuses prior to the 1963 census 5,373 unmarked bass were fin clipped and restocked in Ridge Lake. As any marked fish may survive one or more periods between censuses, the restocking numbers in Tables 14 and 15 show a total somewhat larger than the total number of bass actually fin clipped. Of the fish restocked, about 59 percent were caught by fishermen, 18 percent were recovered in succeeding draining censuses, and only 23 percent disappeared. Periods between marking and recensusing were 2, 3, and 4 years.

Table 14. — Rates of exploitation and unaccountable losses of marked largemouth bass in Ridge Lake.[a]

Period	*Total Marked Bass of Each Period*	*Marked Bass Per Hectare*[b]	*Percent Recoveries and Losses*	*Annual Exploitation Rate,*[c] *Percent*
1941–1943				
1941 Original Stock	435	60	0.0	0.0
1942 Creel	41	6	9.4	9.4
1943 Census	17	2	3.9	0.0
Unaccountable loss	*377*	*52*	*86.7*	*0.0*
1943–1945				
1943 Restocking	1,515	208	0.0	0.0
1944 Creel	469	64	31.0	31.0
1945 Census	553	76	36.5	0.0
Unaccountable loss	*493*	*68*	*32.5*	*0.0*
1945–1947				
1945 Restocking	647	89	0.0	0.0
1945 Creel	404	56	62.4	62.4
1946 Creel	88	12	13.6	36.2
1947 Census	84	12	13.0	0.0
Unaccountable loss	*71*	*10*	*11.0*	*0.0*
1947–1949				
1947 Restocking	392	54	0.0	0.0
1947 Creel	137	19	34.9	34.9
1948 Creel	107	15	27.3	42.0
1949 Census	110	15	28.1	0.0
Unaccountable loss	*38*	*5*	*9.7*	*0.0*
1949–1951				
1949 Restocking	1,027	141	0.0	0.0
1949 Creel	575	79	56.0	56.0
1950 Creel	148	20	14.4	32.7
1951 Census	190	26	18.5	0.0
Unaccountable loss	*114*	*16*	*11.1*	*0.0*

[a] Lake area from 1941 to 1951 restocking, 7.28 ha; from 1951 creel to 1963, 6.88 ha.

[b] Rounded to the nearest whole number.

[c] Exploitation rate is based on theoretical number of marked fish present in the lake at the beginning of the fishing season.

In only a few instances could we finally account for all of the bass in a group of similarly marked fish that were returned to Ridge Lake after a draining census. There were a number of ways, other than being caught, in which a fish might be removed from the population: (i) Some of the smaller marked bass (20–23 cm) may have been preyed upon by larger bass or may have moved out of the lake over the surface spillway in times of floods. (ii) Some bass of all sizes injured in the draining, censusing, and restocking operation may have died some time after restocking and been torn to pieces on the lake bottom; additionally, a very few large bass may have become buried in the soft mud of the lake basin during the late stages of a census and may not have been recovered. (iii) Individual fishes dying of senile degeneration in the period between censuses may have been torn to pieces by crayfish and turtles so that their carcasses never floated to the surface. (iv) Some fish injured by hooking or trapped on broken lines, on lost stringers, or in lost wire or string mesh fish holding baskets may have died and disintegrated without coming to the surface. (v) A few marked bass may have been taken by large bird predators, such

Table 14. — Continued

Period	*Total Marked Bass of Each Period*	*Marked Bass Per Hectare*[b]	*Percent Recoveries and Losses*	*Annual Exploitation Rate,*[c] *Percent*
1951–1953				
1951 Restocking	803	110	0.0	0.0
1951 Creel	486	68	60.5	60.5
1952 Creel	129	18	16.1	40.7
1953 Census	80	11	10.0	0.0
Unaccountable loss	*108*	*15*	*13.4*	*0.0*
1953–1956				
1953 Restocking	604	88	0.0	0.0
1953 Creel	381	55	63.1	63.1
1954 Creel	124	18	20.5	55.6
1955 Creel	12	2	2.0	12.1
1956 Census	29	4	4.8	0.0
Unaccountable loss	*58*	*8*	*9.6*	*0.0*
1956–Fall, 1959				
1956 Restocking	651 (652)[d]	95	0.0	0.0
1956 Creel	346	50	53.1	53.1
1957 Creel	143	21	22.0	46.9
1958 Creel	29	4	4.4	17.9
1959 Creel	10	1	1.5	7.5
1959 Census	41	6	6.3	0.0
Unaccountable loss	*82*	*12*	*12.6*	*0.0*
1960–1963				
1960 Restocking	299	43	0.0	0.0
1960 Creel	44	6	14.7	14.7
1961 Creel	48	7	16.0	18.8
1962 Creel	15	2	5.0	7.2
1963 Census	86	12	28.8	0.0
Unaccountable loss	*106*	*15*	*35.4*	*0.0*

[d] One more marked bass was caught than was recorded as restocked in 1956.

Table 15.— Fishermen's catches and unaccountable losses of Ridge Lake largemouth bass marked in spring draining censuses of 1943, 1945, 1947, 1949, 1951, 1953, 1956, 1959 (fall), and 1963. Numbers in parentheses below restocked fish numbers show average weights (grams) of fish restocked.

Fish Group	*Original Stock*[a]						*1941–1942 Group* (Left Pectoral)		*1943–1944 Group*[b] (Right Pectoral)		*1945–1946 Group* (Left Pelvic)		*1947–1948 Group* (Dorsal)	
	Left Pectoral		Right Pectoral		Dorsal									
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1941 Original stock[a]	58	...	42	...	335	...	...	...	...	...	...	...	...	...
1942 Creel	11	19.0	14	33.3	16[c]	4.8	...	...	...	...	...	...	...	...
1943 Census	3	5.2	12	28.6	2	0.6	...	...	...	...	...	...	...	...
Unaccountable loss	*44*	*75.8*	*16*	*38.1*	*317*	*94.6*	...	...	...	...	...	...	...	...
1943 Restocking	3	...	10	...	2	...	1,500	...	...	...	...	...	...	...
	(1,542)		(1,501)		(1,043)		(77)		...	...	...	...	...	...
1944 Creel	3[d]	100.0	1[d]	10.0	1[e]	50.0	464	30.9	...	...	...	...	...	...
1945 Census	0	0.0	9	90.0	1	50.0	543	36.2	...	...	...	...	...	...
Unaccountable loss	*0*	*0.0*	*0*	*0.0*	*0*	*0.0*	*493*	*32.9*	...	...	...	...	...	...
1945 Restocking	...	...	9	...	...	...	496	...	142	...	...	...	...	...
			(1,769)				(349)		(322)					
1945 Creel	...	...	3	33.3	...	...	337	68.0	64	45.1	...	...	...	...
1946 Creel	...	...	0	0.0	...	...	69	13.9	19	13.4	...	...	...	...
1947 Census	...	...	1	11.1	...	...	63	12.7	20	14.1	...	...	...	...
Unaccountable loss	...	...	*5*	*55.6*	...	...	*27*	*5.4*	*39*	*27.4*	...	...	...	...
1947 Restocking	...	...	1	...	...	...	61	...	20	...	310	...	...	...
			(3,062)				(1,107)		(1,098)		(413)			
1947 Creel	...	...	0	0.0	...	...	18	29.5	3	15.0	116	37.5	...	...
1948 Creel	...	...	0	0.0	...	...	14	23.0	3	15.0	90	29.0	...	...
1949 Census	...	...	1	100.0	...	...	23	37.7	9	45.0	77	24.8	...	...
Unaccountable loss	...	...	*0*	*0.0*	...	...	*6*	*9.8*	*5*	*25.0*	*27*	*8.7*	...	...

[a] Original stock with left pectoral fin clipped was from Crab Orchard Lake, that with right pectoral fin clipped was from Lake Chautauqua, and that with dorsal fin clipped was from Lake Glendale.

[b] Some of the fish of this group were spawned in 1941 or 1942, escaped the 1943 census, and appeared as unmarked fish in the census of 1945, when they were given the same mark as the fish spawned in 1943 and 1944.

[c] One of these fish was taken in 1941.

[d] One of these fish with left pectoral fin clipped and the one with right pectoral fin clipped were taken in 1943.

[e] This fish was found dead July 7, 1943.

Table 15. — Continued

Fish Group	*1941–1942* *Group* (Left Pectoral)		*1943–1944* *Group* (Right Pectoral)		*1945–1946* *Group* (Left Pelvic)		*1947–1948* *Group* (Dorsal)		*1949–1950* *Group* (Left Pectoral)		*1951–1952* *Group* (Right Pectoral)		*1953–1955* *Group* (Dorsal)	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1949 Restocking	. . .	. . .	1 (3,175)	. . .	. . .	. . .	23 (1,796)	. . .	9 (1,687)	. . .	77 (1,188)	. . .	917 (231)	. . .
1949 Creel	. . .	. . .	1	100.0	. . .	. . .	10	43.5	5	55.6	59	76.6	500	54.5
1950 Creel	. . .	. . .	0	0.0	. . .	. . .	0	0.0	0	0.0	0	0.0	148	16.1
1951 Census	. . .	. . .	0	0.0	. . .	. . .	4	17.4	2	22.2	11	14.3	173	18.9
Unaccountable loss	. . .	. . .	*0*	*0.0*	. . .	. . .	*9*	*39.1*	*2*	*22.2*	*7*	*9.1*	*96*	*10.5*
1951 Restocking	3 (2,254)	. . .	2 (2,064)	. . .	9 (1,819)	. . .	170 (894)	. . .	619 (268)	. . .	. . .	. . .	. . .	. . .
1951 Creel	0	0.0	1	50.0	3	33.3	117	68.8	365	59.0	. . .	. . .	. . .	. . .
1952 Creel	0	0.0	0	0.0	0	0.0	2	1.2	127	20.5	. . .	. . .	. . .	. . .
1953 Census	2	66.7	1	50.0	2	22.2	31	18.2	44	7.1	. . .	. . .	. . .	. . .
Unaccountable loss	*1*	*33.3*	*0*	*0.0*	*4*	*44.5*	*20*	*11.8*	*83*	*13.4*	. . .	. . .	. . .	. . .
1953 Restocking	2 (2,767)	. . .	1 (1,996)	. . .	1 (2,268)	. . .	31 (1,433)	. . .	44 (898)	. . .	525 (136)	. . .	. . .	. . .
1953 Creel	0	0.0	0	0.0	0	0.0	12	38.7	21	47.7	348	66.3	. . .	. . .
1954 Creel	0	0.0	0	0.0	0	0.0	7	22.6	12	27.3	105	20.0	. . .	. . .
1955 Creel	0	0.0	0	0.0	0	0.0	1	3.2	0	0.0	11	2.1	. . .	. . .
1956 Census	1	50.0	0	0.0	0	0.0	8	25.8	3	6.8	17	3.2	. . .	. . .
Unaccountable loss	*1*	*50.0*	*1*	*100.0*	*1*	*100.0*	*3*	*9.7*	*8*	*18.2*	*44*	*8.4*	. . .	. . .
1956 Restocking	. . .	. . .	. . .	. . .	. . .	. . .	2 (2,268)	. . .	3 (1,964)	. . .	6 (7) (1,284)	. . .	640 (159)	. . .
1956 Creel	. . .	. . .	. . .	. . .	. . .	. . .	0	0.0	1	33.3	0	0.0	345	53.9
1957 Creel	. . .	. . .	. . .	. . .	. . .	. . .	0	0.0	0	0.0	3	42.9	140	21.9
1958 Creel	. . .	. . .	. . .	. . .	. . .	. . .	0	0.0	0	0.0	0	0.0	29	4.5
1959 Creel	. . .	. . .	. . .	. . .	. . .	. . .	0	0.0	0	0.0	4[f]	57.1	6	1.0
1959 Census (fall)	. . .	. . .	. . .	. . .	. . .	. . .	0	0.0	1	33.3	0	0.0	40	6.2
Unaccountable loss	. . .	. . .	. . .	. . .	. . .	. . .	*2*	*100.0*	*1*	*33.4*	*0*	*0.0*	*80*	*12.5*

[f] One more bass with the right pectoral fin clipped was caught than was recorded in the restocking after the 1956 census.

Table 15.—Continued

Fish Group	1945–1946 Group (Left Pelvic)		1947–1948 Group (Dorsal)		1949–1950 Group (Left Pectoral)		1951–1952 Group (Right Pectorial)		1953–1955 Group (Dorsal)		1956–1959 Group (Left Pectoral)		1960–1962 Group (Right Pectoral)	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1960 Restocking	...	...	...	...	...	...	...	...	14	...	20	...	265	...
									(1,656)		(1,080)		(816)	
1960 Creel	...	...	...	...	...	...	...	...	3	21.4	...	...	41	15.5
1961 Creel	...	...	...	...	...	...	...	...	...	...	...	...	48	18.1
1962 Creel	...	...	...	...	...	...	...	...	...	...	...	...	15	5.7
1963 Census	...	...	...	...	...	...	...	...	11	78.6	13	65.0	62	23.4
Unaccountable loss	...	...	...	...	...	...	...	...	*0*	*0.0*	*7*	*35.0*	*99*	*37.3*

as great blue herons or an osprey that visited the lake occasionally; a few bass may have been taken by poachers at times when the lake was closed to fishing. However, losses of fishes to birds and poachers are considered very minor.

In Table 14 nine periods of 2–3½ years, each delimited by draining censuses, are shown with the numbers of marked bass of all sizes returned after a census, the numbers and percentages of marked fish in the catches of fishermen, the numbers and percentages of marked bass in the next draining census, and the numbers and percentages of marked fish that disappeared between the two censuses.

The annual exploitation rate was calculated by dividing the number of marked fish caught by fishermen during a given season by the number of marked fish that were supposed to be present at the beginning of that fishing season. The exploitation rate for the first fishing season after a census was considered to be the percentage of restocked marked fishes recaptured by fishermen in that season. The exploitation rate for the second fishing season after a census takes into account the fishes taken by angling in the first season, i.e., if 500 fishes were returned and 100 were recaptured in the first fishing season, the exploitation rate for the second season would be based on 400 rather than 500 fishes. The exploitation rate figures have not been adjusted for the unaccountable losses because it was impossible to assign exact times for the occurrence of such losses within the period. Because of the unaccountable losses in intercensus periods, the actual exploitation rates were somewhat higher than shown.

When bass belonging to the various mark groups were separated to show the numbers of each group in successive intercensus periods (Table 15), it was evident that significant variations in the mortality rates of fishes of various sizes and ages were indicated by the unaccountable losses. For example, in the 1941–1942 group (marked left pectoral) the unaccountable losses in the 1943–

1945 period when the fish were still quite small (18–28 cm) was 32.9 percent. In the next two 2-year periods, 1945–1947 and 1947–1949, the fish were 4–8 years old and increased in weight from about 0.34 kg each to about 1.8 kg each. The unaccountable mortality rate for the 1945–1947 period was 5.4 percent and for the 1947–1949 period, 9.8 percent. At least one of these bass lasted for 7 more years, and after 1949 the unaccountable mortality rate again became greater than 30 percent.

This change from high natural mortality among small bass, followed by low mortality until the fish passed the age of 7–8 years, followed again by high mortality among the older fish seemed to be fairly characteristic of most of the mark groups (Fig. 7). These data have been summarized in Table 16. Natural mortality rates among bass greater than 1.8 kg were relatively high in Ridge Lake, and these fish were very difficult to catch with hook and line. It was evident from the data presented in Table 16 that more of these large fish died from natural causes than were caught.

The oldest largemouth recorded at Ridge Lake was a 1941 year-class fish taken in the 1956 draining census at the age of 15 years. Only four of this year-class lived to be 10 years of age.

Table 16. — Natural, nonfishing mortality rates of various weight ranges of marked largemouth bass in Ridge Lake, tabulated at the beginnings and ends of six 2-year periods and three 3-year periods, 1941–1963. Mortality rates for the 3-year periods were not significantly different from those of the 2-year periods.

Weight Range in Kilograms	*Natural Mortality as Average Percent of Marked Bass*
0.07–0.34	33.0
0.35–1.13	13.4
1.14–1.81	14.6
1.82–2.27	39.0
2.28–2.72	72.9

In the 1943–1944 marked group one fish attained the age of 11 or 12 years, in the 1945–1946 group one fish reached the age of 10 or 11 years, and in the 1947–1948 group two fish reached the age of 9 or 10 years. Most of the bass were lost at ages between 7 and 10 years.

The high unaccountable losses in the 1941–1943 period were based on the marked bass originally stocked and were due to the very high death rate of these fish. Apparently many of the adult and yearling bass released in Ridge Lake in the initial stocking in 1941 were injured prior to release, and they probably died within a short time afterwards. This loss has been described in more detail by Bennett (1954*a*:265–266).

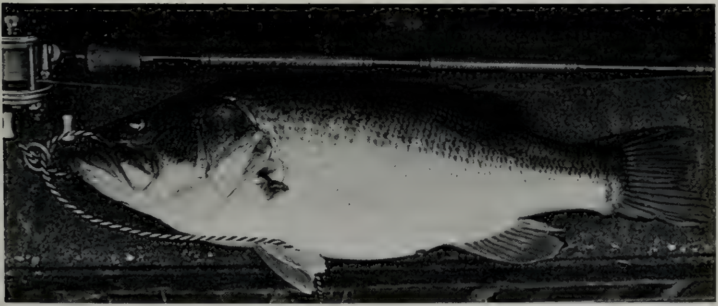

Fig. 7. — Largemouth bass showing partial regeneration of the left pectoral fin that was clipped to mark the fish when the bass was about 22 cm long. This fish had appeared in three draining censuses prior to being caught by a fisherman. It was 56 cm long, weighed 3.0 kg, and was 9 years old when captured.

EFFECTS OF CENSUSING AND OF CULLING SMALL FISHES ON THE EXPLOITATION RATE

The marking and counting of bass and large bluegills returned to the lake following each draining census and the complete creel census made in each fishing season allowed us to compare the exploitation rates of largemouth bass and bluegills in the fishing seasons immediately before and after draining censuses. In postdraining creel censuses the effects of the culling operation were indicated because the March draining eliminated a great many of the small fishes, crayfish, and aquatic invertebrates of value as fish foods. With the impoundment of new water in April and May the numbers of small aquatic animals, including fishes, undoubtedly increased rapidly, but these remained of such small sizes until well into the summer that they were of little interest to the bass of 20 cm and larger. This was not true for bluegills, because all sizes of these fish normally feed on entomostraca and small aquatic insect larvae.

We have assumed that the fishes put back after a census in March comprised the population of catchable-sized fish present in June when the lake was opened to controlled fishing. Table 17 shows the bass and bluegills per hectare released after each of the eight censuses (not including the 1943 census because the lake was not open to fishing in 1943), the fishes caught per hectare in the following fishing season, and the percentages caught of the total numbers and weights of marked fishes. The bass returned in March probably increased in weight very little during April and May because of a shortage of their larger items of food. Bluegills may have achieved average to rapid growth because of the rapid expansion of populations of entomostraca.

Table 17 indicates that the exploitation rates of bass numbers in single fishing seasons following draining and culling operations were usually between 37 and 63 percent. The exploitation rate of bass weight reached as high as 73.7 percent. There was no evidence that such exploitation represented overfishing although the total numbers and weights of bass available for replacement after a census varied a good deal.

Although Table 17 shows that the removal of bass by angling averaged around 56 percent of these fish in most spring draining census years, this was not true in 1960 and 1963. In 1960 the number of bass brought back to Ridge Lake from the hatchery where they had been kept during the winter was comparatively small. In 1963 only 116 large bass were available for restocking, but each of these fish exceeded 1 kg in weight. There was a very noticeable shortage of bass in the length range of 25–35 cm (weight range 0.25–0.45 kg). Bass smaller than 25 cm exceeded 6,000 in the census, and more than 2,000 of these small bass were fin clipped and restocked. Fishermen apparently caught and kept relatively few of these small bass.

In seasons of postcensus fishing the catch of bluegills returned after censusing varied between 32 and 41 percent. An exception occurred in 1963 when 966 bluegills of 15 cm or more in length and 3,500 bluegills of less than 15 cm were returned after the draining. This total restocking of almost 4,500 bluegills was not followed by a proportionately large catch of these fishes.

It was also possible to estimate less exactly the bass and bluegill exploitation rates in summers immediately preceding draining censuses. An estimation of the total populations of bass and bluegills was made by adding the catch figures for the summer in question to the catchable-sized fish found in the draining following that summer. Obviously, large fish in the draining censuses were present in the lake during the preceding fishing summers and were available to the anglers.

Table 18 shows the estimated numbers and weights of bass and bluegills

Table 17.—Percentages of numbers and weights of marked bass and bluegills caught by fishermen in the fishing seasons immediately following draining censuses.

Census Year	*Marked Fish Returned After Census, Per Hectare*				*Marked Fish Caught in Season Following Census, Per Hectare*				*Percent of Available Fish Caught by Anglers*			
	Largemouth Bass		Bluegills		Largemouth Bass		Bluegills		Largemouth Bass		Bluegills	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight
1945	89	32.1	8	1.6	56	22.2	tr[a]	tr	62.9	69.2	. . .	. . .
1947	54	30.3	242	17.7	20	11.6	88	7.0	37.0	38.3	36.4	39.5
1949	141	50.1	0	. . .	79	33.6	2	0.1	56.0	67.1	. . .	. . .
1951	110	47.5	90	8.1	68	35.0	31	4.3	61.8	73.7	34.4	53.1
1953	88	24.1	215	18.6	55	14.5	89	11.4	62.5	60.2	41.4	61.3
1956	95	17.3	146	17.5	50	11.2	47	7.4	52.6	64.7	32.2	42.3
1960 (Fall 1959)	43	9.7	654[b]	17.7	6	2.3	10[c]	0.7	14.0[d]	23.7	. . .	. . .
1963	347	29.5	653	17.8	25	7.1	52	3.3	7.2[e]	24.1	8.0	18.5
							Average[f]		*55.9*	*62.6*	*38.1*	*49.1*

[a] tr = Trace; less than one fish or less than 0.1 kg per hectare.

[b] Hybrid sunfishes stocked from a nursery pond; no bluegills returned to lake.

[c] Hybrid sunfish; catch of hybrids restricted by a 175-mm minimum length.

[d] Bass population abnormally small and in poor physical condition in 1960.

[e] Most of the bass returned after the 1963 census were too small to interest anglers.

[f] Averages exclusive of 1960 and 1963 percentages.

Table 18. — Estimated numbers and weights of bass and bluegills available for angling in seasons prior to draining censuses, numbers and weights of these fish caught, and percentages of available fish taken by anglers.[a]

Precensus Year	*Large Fish Censused Plus Fish Caught in Season Before Census, Per Hectare*				*Fish Caught in Season Before Census, Per Hectare*				*Percent of Available Fish Taken by Angling*			
	Largemouth Bass		Bluegills		Largemouth Bass		Bluegills		Largemouth Bass		Bluegills	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Percent of Number	Percent of Weight	Percent of Number	Percent of Weight
1944	162	52.3	0	. . .	64	16.8	0	. . .	39.5	32.1	. . .	. . .
1946	105	46.2	1,176	83.1	50	16.4	232	14.2	47.6	35.5	19.7	17.1
1948	135	63.7	1,225	91.4	89	28.6	800	51.4	65.9	44.9	65.3	56.2
1950	143	65.6	214	15.7	71	20.6	123	7.5	49.6	31.4	57.5	47.7
1952	134	33.8	1,095	85.0	114	18.1	453	34.8	85.1	53.6	41.4	40.9
1955	225	43.8	1,951	164.9	187	25.5	692	60.7	83.1	58.2	35.5	36.8
1959[b]	100	34.7	1,794	143.6	81	14.9	1,144	84.9	81.0	42.9	63.8	59.1
1962	69	49.0	616	24.9	21	7.3	398	16.0	30.4	14.9	64.6	64.2
							Average		*60.3*	*39.2*	*49.7*	*46.0*

[a] Fishes considered available for angling were bass 25 cm or longer and bluegills 15 cm or longer and some smaller fishes actually caught and kept by anglers.

[b] Census of October 1959.

per hectare in the lake during the summers preceding draining censuses, the numbers caught by angling, and the percentages of total numbers and weights that these catches represented. In contrast to the exploitation rates for bass in draining years, the rates in nondraining years were usually somewhat higher in number, averaging about 60 percent, and lower in weight, with an average of about 39 percent.

Exploitation rates for large bluegills were both larger and smaller than in the postcensus fishing seasons and much less constant. This variation was associated in part with varying numbers of large bluegills available. In some years large bluegills were relatively scarce; in others they were much more abundant. Except in the drawdown period the small bluegills always greatly exceeded large ones in number. In 1948 and 1959 unusually large catches of bluegills were made.

ANGLING AS A TEST FOR MANAGEMENT TECHNIQUES

As described in the section on the creel census, Ridge Lake was opened to controlled public fishing in all years after 1941 except 1943. Table 19 shows the numbers and weights of fishes per hectare taken by angling during these years. Bass removed in 1941 and 1943 were those taken by our own staff to follow the growth of undesirable-sized bass. The catch of 1963 was included to show the number of fishes caught of those returned after the 1963 census.

Table 20 gives the annual intensity of fishing in man-hours per hectare and the seasonal average rate of catch in number and weight of fish per man-hour of fishing. These rates are based on catches of all kinds of fishes. The fishing pressure after the war years reflected in part the attractiveness of the fishing. Fishing pressure reached a maximum of 791 man-hours per hectare in 1948 and exceeded 700 man-hours per hectare through most of the 1950's.

The rate of catch exceeded a seasonal average of one fish per man-hour in 1948, 1955, 1958, 1959, and 1962 (Table 20). Best years from the standpoint of weight of fish caught per man-hour were 1948, 1954, 1955, 1957, 1958, and 1959.

The two best bass fishing seasons were 1949 and 1951. In each of these years the catch was more than 500 bass, weighing 245.1 and 247.4 kg, respectively. After the March 1949 census 1,027 bass weighing 365 kg were returned to Ridge Lake for the 1949 fishing season (Table 2). In the 1949 season we took away the small bass and bluegills and many of the crayfish in the usual biennial culling operation. We also concentrated the larger bass that had developed in 7.28 ha of water surface in a lake of only 4.45 ha surface area, because rainfall in the spring of 1949 was subnormal. The level was down throughout the 1949 fishing season, but the lake refilled in the fall and winter.

Following the 1951 census, 803 bass weighing 345.7 kg were returned to the lake, which filled by the end of June (Table 2). However, as usual in a spring draining year, these fish had a reduced food supply.

In 1949 following the draining and culling, which reduced the food supply of bass, and concentration of bass in a smaller than usual water volume, fishermen took 56 percent of the total bass available and 67 percent of the weight of bass put back (Table 17), which, of course, did not represent the weight available at any instant during the 1949 season.

Similarly, in 1951 fishermen took nearly 62 percent of the bass available and 74 percent of the weight of bass returned after the census (Table 17).

In 1950 and 1952, after the exceptional yields of bass in 1949 and 1951, the numbers of bass caught by anglers were not significantly lower (515 and 784, respectively), but the weight of the bass caught was lower because the faster-growing bass (cannibals) of the

Table 19.—Largemouth bass, bluegills, warmouths, channel catfish, and other fish permanently removed from Ridge Lake by angling, 1941–1963.

Year	*Largemouth Bass, Per Hectare*		*Bluegills, Per Hectare*		*Warmouths, Per Hectare*		*Channel Catfish, Per Hectare*		*Other Fish, Per Hectare*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
1941	7	0.5	0	. . .	0	. . .	0	. . .	0	. . .
1942	67	16.9	0	. . .	0	. . .	0	. . .	0	. . .
1943	4	1.1	0	. . .	0	. . .	0	. . .	0	. . .
1944	64	16.8	0	. . .	0	. . .	0	. . .	4	2.3
1945	56	22.2	tr[a]	tr	0	. . .	0	. . .	1	0.3
1946	50	16.4	232	14.2	0	. . .	0	. . .	39	2.8
1947	25	12.2	88	7.0	0	. . .	0	. . .	5	0.4
1948	89	28.6	801	51.4	0	. . .	0	. . .	33	6.5
1949	82	33.7	2	0.1	tr	0.1	0	. . .	tr	0.1
1950	71	20.6	123	7.5	7	0.3	0	. . .	31[b]	5.0
1951	75	36.0	122	9.3	7	1.0	21	4.4	tr	0.4
1952	114	18.1	453	34.8	10	1.3	20	9.4	5	0.7
1953	76	16.9	110	12.2	10	1.8	18	9.2	1	0.1
1954	178	23.4	239	27.5	11	2.2	17	16.0	6	0.8
1955	187	25.5	692	60.7	74	7.4	4	4.9	3	0.4
1956	81	13.0	218	25.2	15	1.8	12	16.6	8	2.2
1957	213	30.5	526	44.0	51	5.9	5	11.0	20	4.0
1958	118	16.0	722	47.4	36	1.6	11	4.6	5	1.4
1959	82	14.9	1,144	84.9	116	9.2	12	7.8	1	0.2
1960	6	2.3	0	. . .	0	. . .	tr	0.3	9[c]	0.7
1961	13	5.6	20	0.6	3	0.5	tr	1.9	29[d]	3.4
1962	21	7.3	398	16.0	15	0.7	0	. . .	176[e]	14.8
1963	43	12.7	52	3.3	7	0.3	0	. . .	2	0.1
Total	*1,722*	*391.2*	*5,942*	*446.1*	*362*	*34.1*	*120*	*86.1*	*378*	*46.6*

[a] tr = Trace; less than one fish or less than 0.1 kg per hectare.
[b] These fishes were 36 green sunfish weighing 2.13 kg and 187 black bullheads weighing 66.92 kg.
[c] Bluegill x warmouth hybrids, 178 mm or longer.
[d] These fishes were 194 bluegill x warmouth hybrids and 6 red-ear x warmouth hybrids.
[e] These fishes were 1,075 bluegill x warmouth hybrids and 134 red-ear x warmouth hybrids.

preceding year-classes made up much of the catch.

On the basis of the catch of bass by anglers in 1948 and 1950 we must assume that large numbers of bass were present in those years. Otherwise, the potential would not have been present for the superior bass fishing of 1949 and 1951. The fact that superior bass fishing reoccurred in 1951 after an outstanding year in 1949 indicates that bass are capable of replacing their populations of useful-sized fish very rapidly provided there is sufficient survival to replace those taken but not such excessive survival of a year-class as to create overpopulation and stunting.

When a program of biennial draining is in operation, the spawning season following a March draining may see the production of excessive numbers of young bass. The cannibals and other faster-growing individuals of this year-class will, if not taken by anglers or otherwise killed, be incorporated into the population at the time of the next draining and censusing; also, at this time the bass that have failed to grow to at least 20 cm in two growing seasons will be eliminated through the culling operation, and even the number of bass exceeding 20 cm may be reduced if we find a total population of more than 2,000 bass, or around 280–290 per hectare.

With the exception of the fishing season of 1948, bluegill yields during the 10-year period of biennial draining and

Table 20. — Annual intensity of fishing in man-hours per hectare and seasonal average rate of catch in number and weight of fish per man-hour of fishing in Ridge Lake, 1942–1963.

Year	*Man-Hours of Fishing Per Hectare*	*Catch Per Man-Hour*	
		Number	Weight in Grams
1942	524	0.1	32
1944[a]	222	0.3	76
1945[b]	260	0.2	86
1946	415	0.8	80
1947[b]	383	0.3	51
1948	791	1.2	109
1949[b]	544	0.2	62
1950	554	0.4	60
1951[b]	751	0.3	68
1952	714[c]	0.8	90
1953[b]	455	0.5	88
1954	702	0.6	100
1955	731	1.3	135
1956[b]	714	0.5	82
1957	786	1.0	121
1958	704	1.3	101
1959	768	1.8	152
1960[b]	240	0.1	14
1961	410	0.2	29
1962	410	1.5	95
1963[b]	264	0.4	62

[a] Ridge Lake was closed to public fishing in 1943 after spring draining.

[b] Lake drained and population culled of small fish in early spring prior to fishing season, except that lake was drained in October 1959, left dry during winter, and restocked in spring of 1960.

[c] After 1951 lake surface area estimated at 6.88 ha.

culling were small. In 1948 fishermen caught 5,800 bluegills; in other years of this period fewer than 1,700 bluegills were caught. This was partly due to the severe culling of bluegills of all sizes at each census. Excessive numbers of small bluegills are good for little except to cause slow growth among all sizes of bluegills, and in most years the bass seemed unable to provide any degree of control of this species. For these reasons it was customary to return fewer than 2,000 bluegills to Ridge Lake after a census. Exceptions were 1960 when 4,500 hybrid sunfishes were stocked to replace the former bluegill population and 1963 when 4,500 bluegills were returned.

The best bluegill fishing seasons after 1951 were 1952, 1955, 1957, 1958, and 1959, with the largest catch being made in 1959 when 7,868 of these fish, weighing 584.1 kg (1,144 per hectare weighing 84.9 kg), were taken. Two of these superior bluegill seasons were during the period of drawdowns (1952, 1955) and three were in the period of stable water levels (1957, 1958, and 1959).

Again, hunger appeared to influence the catch of fish. It has been shown in a preceding section that fewer small bluegills and more bluegills of desirable sizes were present during the drawdown period, 1951–1956, than at any other time. We have also shown that there were almost *twice* as many bluegills of desirable sizes in the 1956 census, after 3 years of moderate drawdowns, as there were in any other census except that of 1947. In spite of this fact the yield of large bluegills in 1955 (3,437) prior to the 1956 spring census was second to that taken in 1959 (5,475) after four seasons of stable water levels. In this latter season there were 92,600 bluegills of all sizes in Ridge Lake (13,469 per hectare), and they were competing for the available food supply. In 1955 with only around 22,000 present (about 3,200 per hectare) the competition for food must have been much lessened. The severity of the competition for food was reflected in a higher rate of catch in 1959 than in 1955 and a slightly higher rate of fisherman use in 1959 (Table 20).

WARMOUTHS IN RIDGE LAKE

As described in the introductory pages, adult warmouths were stocked in Ridge Lake in the spring of 1949. These fish first appeared in the catch in 1950 and some were taken in every fishing season except that of 1960 (Table 21). The fact that warmouths appeared in Ridge Lake again after the lake basin remained dry for several months over the winter of 1959–1960 suggests that warmouths and bluegills may have wintered in the same water area, possibly somewhere in Dry Run Creek.

Warmouths were of interest to fishermen because they often were caught on small surface plugs and artificial

Table 21.—Warmouths taken by fishermen, 1950–1963, showing large and small fish, numbers and weights per hectare, and man-hours of fishing per hectare.

Year	*15 cm or Larger*		*Less Than 15 cm*		*All Warmouths*		*Number Per Hectare*	*Weight in Kilograms Per Hectare*	*Man-Hours of Fishing Per Hectare*
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms			
1950	3	0.5	50	1.4	53	1.9	7	0.3	554
1951	51	6.8	0	. . .	51	6.8	7	1.0	751
1952	63	8.8	6	0.4	69	9.2	10	1.3	714
1953	68	12.2	1	0.1	69	12.3	10	1.8	455
1954	72	15.1	2	0.1	74	15.2	11	2.2	702
1955	405	45.3	104	5.8	509	51.1	74	7.4	731
1956	105	12.3	0	. . .	105	12.3	15	1.8	714
1957	211	36.0	139	4.7	350	40.7	51	5.9	786
1958	20	2.2	227	9.1	247	11.3	36	1.6	704
1959	549	49.5	246	13.7	795	63.2	116	9.2	768
1960	0	. . .	0	. . .	0	. . .	0	. . .	240
1961	21	3.4	0	. . .	21	3.4	3	0.5	410
1962	13	2.6	89	2.2	102	4.8	15	0.7	410
1963	0	. . .	49	2.4	49	2.4	7	0.3	264

Table 22. — Channel catfish taken by fishermen, 1951–1963, showing large and small fish, numbers and weights per hectare, and man-hours of fishing per hectare.

Year	*30 cm or Larger*		*Less Than 30 cm*		*All Channel Catfish*		*Number Per Hectare*	*Weight in Kilograms Per Hectare*	*Man-Hours of Fishing Per Hectare*
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms			
1951	0	...	143	30.2	143	30.2	21	4.4	751
1952	138	64.4	0	...	138	64.4	20	9.4	714
1953	121	63.5	0	...	121	63.5	18	9.2	455
1954	120	110.3	0	...	120	110.3	17	16.0	702
1955	27	33.6	0	...	27	33.6	4	4.9	731
1956	86	114.3	0	...	86	114.3	12	16.6	714
1957	33	75.4	0	...	33	75.4	5	11.0	786
1958	36	25.4	37	6.1	73	31.5	11	4.6	704
1959	80	52.2	6	1.4	86	53.6	12	7.8	768
1960	2	1.8	0	...	2	1.8	tr[a]	0.3	240
1961	5	13.2	0	...	5	13.2	tr	1.9	410
1962	0	...	0	...	0	...	0	...	410
1963	0	...	0	...	0	...	0	...	264

[a] Trace; less than one fish or less than 0.1 kg per hectare.

flies, and these fish were much heavier than bluegills for any given length. The anglers' catch was usually comparatively small (Table 21). As with bluegills, the largest catches of desirable-sized warmouths were made in 1955 and 1959.

CHANNEL CATFISH IN RIDGE LAKE

In the opening pages we described the several introductions of channel catfish, the first in May 1951 and others in the fall of 1952 and the winter of 1957. Usually a stocking consisted of about 450–700 fish (62 to somewhat less than 100 per hectare).

At Ridge Lake only a few anglers fished for these catfish (with specialized baits), and usually catches were accidental. Most of the channel cats were caught on night crawlers, *Lumbricus terrestris,* and live or dead minnows. Table 22 shows the catches of channel catfish made in the fishing seasons of 1951–1963, inclusive.

Some channel catfish were accidentally injured or killed during every draining census, partly because of their behavior. They demonstrated a strong tendency to remain in the lake basin instead of moving through the gate valve with the outgoing water. As a consequence, many of these fish were suffocated before they could be placed in the holding basin for live fishes. In addition, 131 catfish died in the hatchery pond at Mattoon over the winter of 1959–1960. When we add to the 834 channel cats caught by anglers the 13 found in the 1963 census and the 212 lost in other operations, the catfish that were accountable amounted to 1,059 of the 1,747 stocked in Ridge Lake, giving a return of 60.6 percent over a 13-season period. This must be considered a very reasonable return on wild fish trapped in the Mississippi River, handled, and hauled several hundred kilometers by tank truck.

Channel catfish grew well in Ridge Lake (Fig. 8). The 13 fish taken in the 1963 census had an average weight of almost 4.45 kg, and the largest weighed 7.71 kg.

The greatest weight of channel catfish was taken by angling in 1956; the catch was 86 fish weighing 114.3 kg. This catch represented 28.6 percent of the total weight of all fishes caught at Ridge Lake in 1956.

Catches of channel catfish after stockings of 60–100 per hectare in Ridge Lake exceeded those of Crance & McBay (1966) in Alabama where 247–492

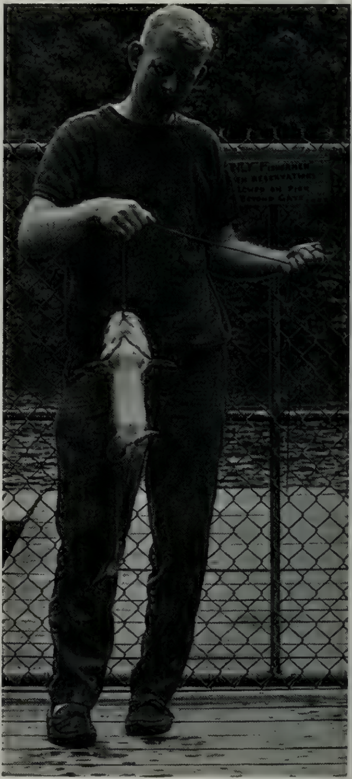

Fig. 8. — Channel catfish caught at Ridge Lake. Catfish are considered a bonus fish by Ridge Lake anglers.

per hectare were stocked along with established populations of bass and bluegills. It is probable that the advantage shown by the Ridge Lake experiment may have been because the channel cats there were 180–300 mm long when stocked, while those stocked by Crance and McBay were only 76–200 mm long, well within the size range for bass forage.

OTHER FISHES IN RIDGE LAKE

As mentioned previously, other fishes in Ridge Lake were mostly green sunfish, black and yellow bullheads, and carp. When both bluegills and hybrid sunfishes were present, the hybrids are included in the "Other Fish" column of Table 19. On several occasions the total weight of "Other Fish" taken by angling exceeded 23 kg and may be of particular interest. For example, the catch in this category in 1948 amounted to 47.1 kg, of which 33.1 kg were black bullheads averaging almost 0.45 kg. These bullheads were all of about the same size and probably represented a single year-class and perhaps part of a single school of bullhead fry produced in the lake or in a Dry Run Creek pool.

In 1950, 187 black bullheads were caught along with 36 green sunfish, but the bullheads were considerably smaller than those caught in 1948, and two size classes were present. Black bullheads and green sunfish nearly disappeared after 1953 although 117 black bullheads were in the catch of 1957 along with one carp and 19 bluegill x warmouth hybrids of small sizes. The 1957 bullheads were of two size categories; 86 were longer than 200 mm and their total weight was 24 kg; 31 smaller bullheads averaged 318 grams.

The fishes in the "Other Fish" column in 1961 and 1962 were hybrid sunfishes and were supposed to be the only sunfishes in the lake. In the 1961 catch 194 bluegill x warmouth and 6 red-ear x warmouth hybrids totaled 23.4 kg. In 1962 the catch was 1,075 bluegill x warmouth hybrids weighing 94.8 kg and 134 red-ear x warmouth hybrids weighing 6.8 kg. Many more of these had been caught in 1961 and thrown back because they were less than the then-required 180 mm total length.

In general one may say that black bullheads and green sunfish were considerably more numerous in the lake prior to the introduction of warmouths and channel catfish. Whether this was in any measure due to competition from the introduced species is unknown.

RELATIONSHIPS BETWEEN THE FISH POPULATION AND THE HOOK-AND-LINE CATCH

We assume that there is a positive relationship between the catch of fishes by anglers and the population of fishes from which the catch is taken; this vari-

Table 23. — Yields per hectare of all fishes taken by anglers from Ridge Lake, 1942–1963, and man-hours of fishing effort. The lake was not open to public fishing in 1941 and 1943.

Year	*Yield in Kilograms Per Hectare*	*Fishing Intensity in Man-Hours Per Hectare*
1942	16.9[a]	524
1944	19.1[a]	222
1945	22.6[a]	260
1946	33.4	415
1947	19.6[b]	383
1948	86.5[c]	791
1949	34.0	544
1950	33.4[b]	554
1951	51.1	751
1952	64.3	714
1953	40.2	455
1954	69.9	702
1955	98.9[c]	731
1956	58.8	714
1957	95.4	786
1958	71.0	704
1959	117.0[c]	768
1960	3.3[d]	240
1961	12.0[d]	410
1962	38.8	410
1963	16.4[b]	264
Average	*47.7*	*540*

[a] Population composed largely of bass; these years omitted from averages.
[b] Poor years for angling.
[c] Good years for angling.
[d] Hybrid sunfishes catch restricted; bass and channel catfish recovering from overwintering in hatchery pond; bluegills nearly absent.

able relationship is affected by species composition, size distribution, density, and behavior of the species involved.

At Ridge Lake there was a great deal of variation in hook-and-line yields during the 21 seasons covered by this report when the lake was opened to controlled public fishing (Table 23). From 1941 to 1945 the fish population of Ridge Lake was composed mainly of largemouth bass, and this was reflected in the catches of 1942, 1944, and 1945. After 1945, when numbers of both bass and bluegills were present, the yields ranged from a low of 3.3 kg per hectare in 1960 to a high of 117.0 kg per hectare in 1959, with an average annual yield of 47.7 kg per hectare.

The extent of use of the lake for fishing varied directly from season to season as the catch varied. Generally, in years when large weights (and numbers) of fishes were caught, the fishing intensity increased, and vice versa. The average fisherman-use level for post-World War II years was 574 man-hours per hectare per season with a range of 240–791. Good and poor fishing years might be defined on the basis of rate of catch and total numbers and weights of fish caught by anglers. These criteria used at Ridge Lake failed to reflect the success of bass fishing in any year.

To explore further the relationships between composition of the fish population and catch, we selected 3 of the poorest fishing years, 1947, 1950, and 1963, when the rates of catch per man-hour were

Table 24. — Composition of the anglers' catch at Ridge Lake for 3 of the poorest years of fishing. All data are per hectare.

Species	*1947 (383 Man-Hours Per Hectare)*		*1950 (554 Man-Hours Per Hectare)*		*1963 (264 Man-Hours Per Hectare)*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
Largemouth bass						
Large[a]	20	11.6	32	16.0	10	12.2
Small[a]	4	0.6	38	4.6	33	0.5
Bluegills						
Large	57	5.9	58	5.2	40	2.2
Small	31	1.1	65	2.3	12	1.1
Warmouths						
Large	0	...	tr[b]	tr	0	...
Small	0	...	8	0.3	7	0.3
Channel catfish						
Large	0	...	0	...	0	...
Others[c]						
Large	3	0.3	27	4.9	tr	tr
Small	2	0.1	4	0.1	2	0.1
Total						
Large	*80*	*17.8*	*117*	*26.1*	*50*	*14.4*
Small	*37*	*1.8*	*115*	*7.3*	*54*	*2.0*
Grand total	*117*	*19.6*	*232*	*33.4*	*104*	*16.4*

[a] The definitions of size categories are:

	Large	Small
Largemouth bass	25 cm or longer	Less than 25 cm
Bluegills	15 cm or longer	Less than 15 cm
Warmouths	15 cm or longer	Less than 15 cm
Channel catfish	30 cm or longer	Less than 30 cm
Other fish	Depends upon species	

[b] tr = Trace; less than one fish or 0.1 kg per hectare.

[c] Mostly black bullheads and green sunfish in 1947 and 1950; hybrid sunfishes in 1963.

0.3, 0.4, and 0.4 fishes, respectively, and 3 of the best fishing years, 1948, 1955, and 1959, when the rates of catch were 1.1, 1.2, and 1.6 fishes per man-hour. Details of the composition of the catches in the selected poor and good fishing years are shown in Tables 24 and 25.

The most obvious differences in the groupings shown in these two tables are in the numbers of fishes caught. In the 3 poor years the average number of fishes caught each season was 151 per hectare, while in the good years the average number was 1,078 per hectare, or more than seven times as many. These differences were also evident in the average weights of the catches. For the poor years the average weight of the catch was 23.1 kg per hectare; for the good years it was 100.8 kg per hectare. The ratio of large to small fishes caught was about the same in the good fishing seasons as it was in the poor ones.

Length frequency distributions of bluegills and largemouth bass in the contrasted fishing seasons are shown in Tables 26 and 27. While on the average about 69 percent of the bluegills taken in the good fishing seasons were 15 cm or longer, only about 63 percent of those taken in the poor seasons were 15 cm or more (Table 26). However, these differences are not significant.

The length frequency distribution for bass shows that more bass 43 cm and longer were caught in the poor year of 1963 than in any good year and more bass of less than 23 cm (689) were

Table 25. — Composition of the anglers' catch at Ridge Lake for 3 of the best years of fishing. All data are per hectare.

Species	*1948 (791 Man-Hours Per Hectare)*		*1955 (731 Man-Hours Per Hectare)*		*1959 (768 Man-Hours Per Hectare)*	
	Number	Weight in Kilograms	Number	Weight in Kilograms	Number	Weight in Kilograms
Largemouth bass						
Large[a]	50	24.6	26	8.2	42	12.2
Small[a]	39	4.0	161	17.3	39	2.7
Bluegills						
Large	476	31.8	546	51.6	796	67.7
Small	324	19.6	145	9.1	348	17.2
Warmouths						
Large	0	...	59	6.6	79	7.2
Small	0	...	15	0.8	36	2.0
Channel catfish						
Large	0	...	4	4.9	12	7.8
Others[b]						
Large	23	6.0	3	0.4	1	0.2
Small	10	0.5	0	...	0	...
Total						
Large	*549*	*62.4*	*638*	*71.7*	*930*	*95.1*
Small	*373*	*24.1*	*321*	*27.2*	*423*	*21.9*
Grand total	*922*	*86.5*	*959*	*98.9*	*1,353*	*117.0*

[a] The definitions of size categories are:

	Large	Small
Largemouth bass	25 cm or longer	Less than 25 cm
Bluegills	15 cm or longer	Less than 15 cm
Warmouths	15 cm or longer	Less than 15 cm
Channel catfish	30 cm or longer	Less than 30 cm
Other fish	Depends upon species	

[b] Green sunfish and black bullheads in 1948; black bullheads and a few naturally produced hybrid sunfishes in 1955 and 1959.

caught in the good year of 1955 than in any other year of those shown in Table 27. The length frequency distribution for bass caught in 1949 is included in Table 27 because the rate of catch for largemouths in that year exceeded that of any other. However, the overall fish yield for 1949 was not particularly high because very few fish other than largemouth bass were present. In considering the size distribution of bass caught in 1949 and comparing this distribution with others in Table 27, it was evident that more bass 25–37 cm long were caught in 1949 than in any other season shown. At the same time 53 bass were caught that ranged from 41 to 56 cm and from about 0.9 to 2.7 kg each.

In Tables 28 and 29 we have made estimates of the numbers and weights of largemouth bass and bluegills per hectare in poor (Table 28) and good (Table 29) fishing seasons and compared them with numbers and weights per hectare of fishes caught in those same years. Fishes were separated into large and small categories as defined in Tables 24 and 25. In some census years, such as 1947, no small bass or small bluegills were put back after the census. In 1963, another census year, 2,270 small bass were marked and restocked, and some bluegills 13–15 cm were restocked. This restocking of small fishes represents rather large differences in numbers restocked; yet fishing was poor in both years. The years 1948, 1950, 1955, and 1959 all preceded censuses so that it was possible to estimate the total population by adding the fish caught in the preceding fishing season to the population subsequently exposed in the draining census.

Upon comparing the data shown in Tables 28 and 29, it became evident that the higher rates of catch in fish per man-hour were dependent upon the catches of bluegills, and high catches of bluegills combined with high rates of catch were related to large populations of

Table 26. — Length frequency distribution of bluegills caught during "good" and "poor" fishing years at Ridge Lake.

Length Class Center in Centimeters	*Poor Fishing Years*			*Good Fishing Years*		
	1947	1950	1963	1948	1955	1959
			Small Sizes			
7.6		13			42	5
8.9	10	65		10	84	34
10.3	35	120	1	74	84	45
11.4	48	67	8	433	157	210
12.7	71	63	15	812	246	524
14.0	64	143	62	1,033	387	1,575
			Desirable Sizes			
15.2	78	208	211	1,117	914	2,448
16.5	104	121	58	679	1,410	2,414
17.8	204	42	2	940	767	580
19.0	26	27	1	502	386	22
20.3	4	15		216	230	11
21.6		8		15	37	
22.9					11	
24.1					5	
Total	*644*	*892*	*358*	*5,831*	*4,760*	*7,868*
Percent small sizes	35.4	52.8	24.0	40.5	21.0	30.4
Percent desirable sizes	64.6	47.2	76.0	59.5	79.0	69.6

these fish. Bluegill fishing was satisfactory if the estimated bluegill population exceeded 2,500 fish per hectare of which more than 1,000 were 15 cm or longer. However, in 1950 the catch of bluegills was poor in spite of the fact that the lake contained 7,138 of these fish per hectare (Table 3). The poor catch may have occurred because only 149 of the 7,138 bluegills were of desirable sizes (15 cm or longer) and fishermen were soon disappointed by the fact that they were unable to catch bluegills of worthwhile sizes.

Table 30 shows the average numbers of large and small bass and large and small bluegills and their total weights, respectively, per hectare in 3 poor fishing years and 3 good ones. These data are computed from data in Tables 28 and 29. Important differences in bluegill average numbers and weights in

Table 27. — Length frequency distribution of largemouth bass caught during "good" and "poor" fishing years at Ridge Lake.

Length Class Center in Centimeters	*Poor Fishing Years*			*Good Fishing Years*			*Best Year for Bass*
	1947	1950	1963	1948	1955	1959	1949
			Small Sizes				
Less than 22.9	16	177	223	230	689	223	12
22.9	8	54	2	29	271	17	27
24.1	8	48	3	28	146	29	67
			Desirable Sizes				
25.4[a]	10	32	1	49	99	71	107
26.7	8	26	...	32	32	100	83
27.9	12	15	1	48	9	63	62
29.2	10	5	...	47	3	21	43
30.5	23	7	2	41	3	13	32
31.8	13	19	...	17	1	2	11
33.0	11	39	2	21	1	2	17
34.3	7	41	...	8	4	1	13
35.6	13	19	5	22	6	1	25
36.8	14	13	3	19	5	1	20
38.1	5	9	7	16	7	2	13
39.4	5	4	7	11	7	...	9
40.6	6	2	4	5	2	...	15
41.9	2	2	5	10	1	2	8
43.2	6	2	12	5	...	1	4
44.4	3	...	5	4	...	3	10
45.7	1	1	9	3	1	1	7
47.0			3	2		1	4
48.3			1	...		...	1
49.5			1	1		...	3
50.8			...			1	...
52.1			...			...	...
53.3			1			...	...
54.6			1			1	1
55.9			1				
Total	*181*	*515*	*299*	*648*	*1,287*	*556*	*594*
Percent small sizes	17.7	54.2	76.3	44.3	85.9	48.4	17.8
Percent desirable sizes	82.3	45.8	23.7	55.7	14.1	51.6	82.2

[a] Minimum legal size prior to 1951.

Table 28. — Population estimates of largemouth bass and bluegills per hectare in Ridge Lake in 3 of the poorest fishing years, with fishing pressures and rates of catch.

Year	*Species*	*Population Estimate Per Hectare*		*Man-Hours of Fishing Per Hectare*	*Catch Per Hectare*		*Rate of Catch Per Hectare*	
		Number	Weight in Kilograms		Number	Weight in Kilograms	Number Per Man-Hour	Weight in Kilograms Per Man-Hour
1947	Largemouth bass							
	Large[a]	54	30.3		25	12.2		
	Bluegills							
	Large	242	17.7		88	7.0		
1947 Total		*296*	*48.0*	*383*	*113*	*19.2*	*0.3*	*0.050*
1950	Largemouth bass							
	Large	105	61.0		32	16.0		
	Small	38	4.6		38	4.6		
	Total	*143*	*65.6*		*70*	*20.6*		
	Bluegills							
	Large	144	13.4		58	5.2		
	Small	70	2.3		65	2.3		
	Total	*214*	*15.7*		*123*	*7.5*		
1950 Total		*357*	*81.3*	*554*	*193*	*28.1*	*0.4*	*0.051*
1963	Largemouth bass							
	Large	17	22.8		10	12.2		
	Small	330	6.1		33	0.5		
	Total	*347*	*28.9*		*43*	*12.7*		
	Bluegills							
	Large	140	8.3		40	2.2		
	Small	512	9.5		12	1.1		
	Total	*652*	*17.8*		*52*	*3.3*		
1963 Total		*999*	*46.7*	*264*	*95*	*16.0*	*0.4*	*0.061*

[a] The definitions of size categories are:

	Large	Small
Largemouth bass	25 cm or longer	Less than 25 cm
Bluegills	15 cm or longer	Less than 15 cm

Table 29. — Population estimates of largemouth bass and bluegills per hectare in Ridge Lake in 3 of the best fishing years, with fishing pressures and rates of catch.

Year	*Species*	*Population Estimate Per Hectare*		*Man-Hours of Fishing Per Hectare*	*Catch Per Hectare*		*Rate of Catch Per Hectare*	
		Number	Weight in Kilograms		Number	Weight in Kilograms	Number Per Man-Hour	Weight in Kilograms Per Man-Hour
1948	Largemouth bass							
	Large[a]	96	59.7		50	24.6		
	Small	273	25.5		39	4.0		
	Total	*369*	*85.2*		*89*	*28.6*		
	Bluegills							
	Large	740	71.7		476	31.8		
	Small	2,768	76.7		324	19.6		
	Total	*3,508*	*148.4*		*800*	*51.4*		
1948 Total		*3,877*	*233.6*	*791*	*889*	*80.0*	*1.1*	*0.101*
1955	Largemouth bass							
	Large	64	26.4		26	8.2		
	Small	161	17.4		161	17.3		
	Total	*225*	*43.8*		*187*	*25.5*		
	Bluegills							
	Large	1,759	155.8		546	51.6		
	Small	192	9.1		145	9.1		
	Total	*1,951*	*164.9*		*691*	*60.7*		
1955 Total		*2,176*	*208.7*	*731*	*878*	*86.2*	*1.2*	*0.118*
1959	Largemouth bass							
	Large	60	32.0		42	12.2		
	Small	40	2.7		39	2.7		
	Total	*100*	*34.7*		*81*	*14.9*		
	Bluegills							
	Large	1,446	126.4		796	67.7		
	Small	348	17.2		348	17.2		
	Total	*1,794*	*143.6*		*1,144*	*84.9*		
1959 Total		*1,894*	*178.3*	*768*	*1,225*	*99.8*	*1.6*	*0.130*

[a]The definitions of size categories are:

	Large	Small
Largemouth bass	25 cm or longer	Less than 25 cm
Bluegills	15 cm or longer	Less than 15 cm

Table 30. — Estimated average numbers and weights of largemouth bass and bluegills per hectare in Ridge Lake in 3 years when fishing was good and 3 years when fishing was poor.

	Largemouth Bass Per Hectare		*Bluegills Per Hectare*	
	Average Number	Average Weight in Kilograms	Average Number	Average Weight in Kilograms
Poor Years				
Large	59		175	
Small	123		194	
Total	*182*	*41.6*[a]	*369*	*17.1*[a]
Good Years				
Large	73		1,315	
Small	158		1,103	
Total	*231*	*54.6*[a]	*2,418*	*152.3*[a]

[a] These weights may be 10–20 percent higher than the actual weights in the lake at the time of fishing because of weight gains in the uncaptured segments of the population in the time between the catch and the next draining census or between the return of fishes after a census and the catch.

good and poor years are much greater than are differences in largemouth bass numbers and weights. Also clearly evident are the great differences in the numbers of catchable bluegills per hectare in the good and poor years.

THE EFFECTS OF MANAGEMENT TECHNIQUES ON FISH POPULATIONS AND ANGLING

Four operational techniques were followed at Ridge Lake in the 1941–1963 period; the results of one of these (the use of hybrid sunfishes) must be disregarded because circumstances prevented a true test. The others were (i) the biennial draining and culling operation, (ii) the fall drawdowns, and (iii) the period of stable water levels. Each of these operational techniques influenced the catch of fish; they also had marked effects upon the fish populations as exposed by draining censuses.

The period of biennial draining and culling extended over 10 years, and the culling operations could have affected the catch of fish in 1943–1951. However, the lake was closed to fishing in 1943, and so a consideration of fishing results must be limited to the other 8 years.

In all cases fishing during the season immediately following a March draining and culling operation must have been different from fishing during the second fishing season of the biennium because of the spawns of fishes and the growth of fishes to catchable sizes that took place in both years of each 2-year period. Also the period between March 1949 and March 1951 must have been at variance with the others because of the fishes' crowded living conditions in 1949 brought on by the failure of the lake to refill completely. Certainly spawn survival in 1949 must have been lower than usual because of the greater than usual density of the bass population during that season.

One would expect the effects of the first September drawdown of the lake level to be evident in the catch of fishes in the 1952 fishing season. The drawdown of September 1952 undoubtedly had an effect on the fish population exposed in the March draining census of 1953. In view of the facts that not all of the fishes taken in the 1953 draining census were returned to the lake and that the complete draining of the lake changed the food-feeder relationships, it would be unreasonable to consider the 1953 catch as being wholly influenced by the drawdown.

After the 1953 census and fishing season, drawdowns were made in the Septembers of 1953, 1954, and 1955. These drawdowns affected the fishing seasons of 1954 and 1955, and their effects were further exposed in the draining census of 1956. Thus, drawdown-oriented fishing seasons were those of 1952, 1954, and 1955. Of these, that of 1952 was affected by a lake surface area reduction of 69 percent and those of 1954 and 1955 by an area reduction of about 35 percent. These differences had varying effects upon the fish populations (as shown by the censuses of 1953 and 1956) and must have affected the hook-and-line catch also.

The stable water period described elsewhere lasted from April 1956 when the lake had refilled after the March 1956 draining to October 1959 when the lake was again drained. Thus the period of stable waters lasted for three winters and four growing seasons for fishes (April to October). During this period the numbers of fishes were allowed to increase without any culling or the restrictive effect of the drawdown. Fishing in 1956 was more influenced by the spring draining than by the nearly stable water levels that were present during the summer fishing season. However, the constantly stable lake in 1957, 1958, and 1959 must have affected the fish population and the fishing. Thus, the stable water period may be considered to have lasted about 3 years.

In Table 31 an attempt has been made to compare the average catches of desirable-sized bass (25 cm or longer), bluegills, and warmouths (15 cm or longer) made under the three operational techniques described above, including eight seasons of biennial culling, three seasons of annual fall drawdowns, and three consecutive seasons of stable water levels. It is evident from this table that larger average numbers and total weights of bass were taken per season during the period of biennial culling than under the other management techniques. Annual fall drawdowns stimulated annual spawns of largemouth bass and increased the numbers of small ones without apparently improving the catch of large bass. The catch of large bass was even smaller under stable waters than under the influence of drawdowns. This reduced catch may have been the result of a large, constantly available supply of small bluegills suitable for bass forage; however, the draining census of 1959 showed that only 124 bass longer than 24.9 cm were present after the four growing seasons of stable waters (Table 8) although 651 bass longer than 20 cm were put back after the census of 1956 (Table 2). This reduction in mature bass indicates that the bass population was not holding its numerical strength during this period.

Table 31. — Average numbers and weights of fish of desirable sizes caught in Ridge Lake under three systems of management.

Number of Years	*Management Practice*	*Average Annual Catch of Fish Per Hectare*								
		Largemouth Bass 25 cm or Longer			Bluegills 15 cm or Longer			Warmouths 15 cm or Longer		
		Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams	Number	Total Weight in Kilograms	Average Weight in Grams
8	Biennial draining	47	19.2	408	133	13.0	98	0	. . .	. . .
3	Annual fall drawdowns	30	11.7	390	304	33.2	109	27	3.4	126
3	Stable water levels	27	12.1	448	472	41.9	89	37	4.3	116

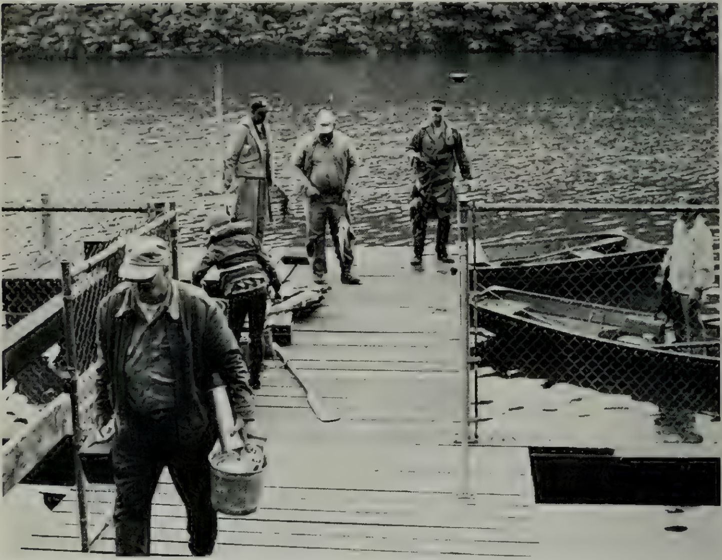

Fig. 9. — Fishermen with their catches on the laboratory pier. Their fish are weighed, measured, and "scaled" for age determination. These data, the time spent in fishing, and the kinds of bait and tackle used are recorded on individual creel cards. When all of this information has been collected for each fisherman, his state fishing license, which has been held at the laboratory, is returned to him.

The greatest average numbers and weights of bluegills and warmouths were caught under stable water conditions (Fig. 9) although the average sizes of the fishes caught were greater during the drawdown period. As mentioned previously, the large catch in the stable water period probably was the result of high population density and food competition; the draining census indicated that bluegills and warmouths of desirable sizes were more numerous during the drawdown period. With the constant gradual buildup of bluegills during the stable water period, the bluegill population might have eventually become so dense as to cause severe food competition and stunting. This competition would have created a situation in which many bluegills might have been caught but few would have been of desirable sizes.

DISCUSSION

The study of the management of the fishes of Ridge Lake over the period 1941–1963 (which still continues) is possibly the longest continuous investigation ever made of a warmwater fish population in a small artificial lake. In this 23 years the lake was drained completely and the fish population was censused nine times. Following these censuses certain numbers and sizes of fishes of one or several species were returned to the partially reflooded lake basin above the dam and the lake basin was allowed to refill.

Each summer, except for those of 1941 and 1943, the lake was opened to controlled public fishing to allow us to gather a complete record of fishing; number of fishermen; time spent; catch by species, numbers, and sizes; and kinds of tackle and baits used, including a comprehensive breakdown of types and colors of a huge variety of artificial fish lures. Data presented in this paper do not include an analysis of fishing other than the time spent in fishing and the catch of fishes, and these are cited for their relevance to the management techniques that were applied. The real test of management lies in the relative numbers and sizes of fish caught under each system.

No attempt has been made to include growth data based on scale collections made from creel censuses and during lake drainings since 1951. Some of these scales were read to furnish growth data shown in the report of 1954 (Bennett 1954*a*). Comparative growth of the important species of fish in Ridge Lake under various management techniques will be presented in a future paper.

The fish population of Ridge Lake has shown a great deal of variability in species abundance, size distribution, and standing crops and has demonstrated the complexity of fish population dynamics. This complexity suggests that one might question the validity of certain types of "results" from population studies of short duration. Present and future observations of the responses of this warmwater fish population to new management practices will be particularly valuable because of the backlog of data dealing with this population's past variations.

At the time the Ridge Lake study was begun, fishermen generally held the misconception that natural reproduction and survival were inadequate to maintain populations of game fishes and panfishes and that an annual stocking of fingerlings was necessary to insure good fishing. Now, 27 years later, no one familiar with fisheries literature believes that natural reproduction of warmwater fishes is unable to maintain their populations. Thus, one of the original purposes of the study has disappeared: that of testing the natural fecundities of several important species of warmwater fishes.

In this connection it is of some interest to note that the 435 largemouth bass released in Ridge Lake in 1941 were the only source of 29,700 bass that have been permanently removed from the lake since then (1941–1967) and that the 129 bluegills released in 1944 have produced more than 400,000 living offspring of which 390,000 have been permanently removed. These figures for the two species probably indicate something of their relative abilities to expand their populations in Ridge Lake, i.e., the bluegills in this environment were at least 10 times as effective in expanding their populations as were largemouth bass. Within this bass-bluegill complex, warmouths stocked in 1949 (138 fish) produced no more than 10,000 fish (6.5 cm and larger) in 18 years.

As was expected, channel catfish failed to reproduce successfully in Ridge Lake. A stream fish that grows well in lakes, the channel cat must have special spawning conditions or it cannot maintain its numbers. One channel catfish fingerling was captured in one draining census, indicating that these fish had attempted to reproduce or gained access to the lake by some other means.

Black bullheads, yellow bullheads, carp, white suckers, and green sunfish were indigenous to the Ridge Lake watershed and were exposed as inhabitants of Ridge Lake in one or more draining censuses; black bullheads and green sunfish were sometimes caught by fishermen. However, the removal of these fishes whenever they appeared in a draining census was sufficient to keep them from significantly increasing their populations. For unknown reasons, green sunfish and black bullheads were much less common in the census of 1953 and thereafter than they had been in the period 1941–1951.

After we compared fishermen's catches made in a season immediately prior to a draining census with the fishes exposed in the draining census, it became evident to us that one should use caution in appraising a fish population on the basis of the annual hook-and-line catch. For example, in 1962 fishermen caught 145 bass, of which 80 were between 25 and 45 cm and the rest smaller. This was a poor catch of bass, and fishermen agreed openly that the lake contained no large ones. When the lake was drained in March of the following year, it was found to contain 90 bass ranging in length from 46 to 58 cm and in weight from 1.6 to 4.1 kg; in fact, 11 bass belonged to the oldest fin mark group (8–10 years old) and averaged more than 2.9 kg. For unknown reasons fishermen had been unable to catch these large fish.

The concept presented by Swingle & Smith (1938, 1939) that single species or mixed populations of warmwater fishes build up to a maximum constant weight within one growing season and then remain at about that weight for an indefinite time has not been demonstrated by the Ridge Lake censuses. Largemouth bass total weights have varied from 240 kg to 412 kg (exclusive of the 1953 census after 2 years of severe drawdowns, when the bass weight was 205 kg); bluegill total weights have ranged from 709 to 1,578 kg, and the total weight for all fishes has varied (after 1945 and exclusive of 1953) from a low of 1,336.7 kg to nearly double that amount–2,092.5 kg (Table 1).

In view of such large variations in standing crops of fishes at Ridge Lake, it seems ridiculous to assume that fish populations remain constant in total weight or that annual hook-and-line yields do not vary greatly. D. Homer Buck and Charles F. Thoits have found similar unexplained variations in single-species populations of fishes in 0.4-ha ponds (personal communication 1968 and in press).

Saila (1958) published a paper using Ridge Lake data from the 1954 report (Bennett 1954*a*) in which he attempted to demonstrate mathematically that a size limit on largemouth bass would eventually assure a greater number of large fish in the catch than was possible without a size limit. In the early years of fishing at Ridge Lake (1942, 1944, and 1945) we imposed a minimum length limit of 25 cm (10 inches), while beginning in 1946 fishermen were asked to bring in all bass regardless of length. This change in policy resulted in periods with and without length limits on bass.

However, these periods were also marked by different culling lengths for bass in the draining censuses, a point apparently not recognized by Dr. Saila. After about half of the stunted 1941 brood of bass (average length about 18 cm) were removed in the 1943 census, the minimum culling length was 25 cm (10 inches) in the 1945 and 1947 censuses, followed by 23 cm (9 inches) in the 1949 census and 20 cm (8 inches) in the 1951 census. These lengths were represented by the following average weights for the smallest bass returned to the lake after these censuses: in 1945, 142 fish averaged 0.33 kg (0.72 pound); in 1947, 310 fish averaged 0.41 kg (0.91 pound); in 1949, 917 fish averaged 0.23 kg (0.51 pound); and in 1951, 619 fish averaged 0.27 kg (0.59 pound). These differences in sizes and numbers of fish returned were great enough to influence the numbers and sizes of fish caught by anglers, and it was simply circumstance that controlled the timing of the periods when length limits were enforced and when they were taken off to match the larger and smaller bass culling sizes.

In comparing populations of largemouth bass and bluegills exposed in the nine censuses, it was of particular interest that the bass population equaled or approached 56 kg per hectare in four of the censuses, once when the lake contained a nearly pure culture of bass and twice when numbers of bluegills were present. This suggests that 56 kg per hectare may be about the maximum carrying capacity of the lake for bass.

No comparable maximum for bluegills was suggested by the census data. The heaviest population of bluegills was found in the census of 1947 when 216.7 kg per hectare were present. The next largest population by weight appeared in 1959 after four growing seasons of constant water levels when 181.2 kg per hectare of bluegills were present. Other censuses showed lesser weights of bluegills.

There appeared to be an inverse relationship between weights of bass and bluegills ($r = -0.91$). The lowest weights of bluegills (exclusive of the drawdown period) were present when bass weights were highest and vice versa.

The biennial draining operations with the culling of all bass of less than 25, 23, or 20 cm and all bluegills except 1,000–4,500 of the larger ones resulted in a buildup of desirable-sized bass and relatively high hook-and-line catches of these fish. This management technique did not stimulate the development of large bluegill populations, and with one exception seasonal catches of bluegills were much less than 50 kg per hectare.

Severe early fall drawdowns that reduced the lake surface area by 69 percent reduced the total weight of the fish population but not in proportion to the lake surface area or volume reduction. More moderate fall drawdowns (3 meters, 35-percent surface area reduction) had no significant effect on the total weight of fish. The drawdown technique appears to be the single most important tool in the management of warmwater fish populations inhabiting lakes that can be artificially reduced in area by the release of water.

Prior to 1956 we believed that a 50-percent reduction in lake surface area was necessary to effect significant changes in a fish population. After the 1956 draining census which followed 3 successive years of moderate September drawdowns (35-percent reduction of the lake surface area) it was obvious that drawdowns to reduce the lake surface area by less than 50 percent were having a beneficial culling effect upon the smaller sunfish species of Ridge Lake without causing any significant reduction in the overall weight of fish that the lake was supporting (Table 3). Bass in the 1956 census were represented by a larger total weight of small fish (less than 25 cm total length) than in any other census except that of 1943 and a smaller weight of large fish than in any preceding census except those of 1943 and 1953 (Table 8). After the mild drawdowns the lake was supporting a substantial population of small bass due to the annual culling action of the drawdowns on the small sunfishes (largely bluegills) that might attack bass fry and limit their survival.

The severe drawdowns of 1951 and 1952 caused a drastic reduction in bluegills so that only 7,500 (1,087 per hectare) were present in the 1953 census (Table 3). More than half of these were larger than 15 cm and the rest smaller (Table 9), giving a catchable population of about 640 bluegills per hectare. According to our creel records, this population of large bluegills was numerically too small to give satisfactory bluegill fishing (one or more fish per man-hour). After the period of moderate drawdowns in 1953, 1954, and 1955 the bluegill population numbered 17,180 (2,497 per hectare) (Table 3) of which slightly more than half (8,661, or 1,258 per hectare) were of desirable sizes (Table 9).

Bluegill fishing was quite good in 1955 (a year prior to a draining census; the catch was almost one fish—0.94—per man-hour), and the bluegill population contained more large fish than in any other year of the 19 years when bluegills were present in Ridge Lake. The fact that the fishermen's catch of bluegills in several other years exceeded that of 1955 suggests that a certain amount of food competition is important in the production of high pole-and-line yields. The knowledge of how to produce superior numbers of catchable-sized bluegills has been carried further since 1963 in a study which will be reported at a later date (Fig. 10).

Many small artificial reservoirs receive heavy human use, and as a consequence the normal fish predators, such as herons, kingfishers, cormorants, and other wild fish-eating birds, are scarce or absent. Also in recent years the numbers of fish-eating birds are believed to have become considerably smaller than formerly because of their reduced fecundity reportedly caused by their ingesting pesticides carried by fishes (Wurster & Wingate 1968). This reduction in the numbers of fish predators has removed a natural check on overpopulation, giving the drawdown technique increased importance as a population regulator. One of the problems associated with drawdowns is to educate fishermen to the usefulness of an annual or biennial water release which may leave unsightly mud flats around the lake edges in early fall and winter. Hopefully, the reservoir will refill again by the next fishing season when the improvement in the fish population will be reflected in better fishing.

There is no longer any question whether a drawdown will cull certain kinds of the smaller fishes in a population, an action always followed by improved survival of bass fry. This observation has also been recorded by Pierce, Frey, & Yawn (1965) in their drawdowns of Georgia ponds and by Lantz, Davis, Hughes, & Schafer (1967) in their drawdowns of Louisiana reservoirs.

Whether these fry will survive in proportional numbers to augment the adult bass population is related to the abundance of predators of fingerling and yearling bass. However, the evidence indicates that bass are most vulnerable to predation in the embryo, yolk-sac fry, free-swimming fry, and small fingerling states, i.e., from the time the eggs are laid to the time the small bass are about 25 mm long. During this period they may be affected adversely by weather changes and they are vulnerable to attack by small fishes (such as stunted bluegills) and predacious aquatic insects. When they reach lengths approximating 50 mm, they become strong swimmers and are too large to be eaten by fishes other than the fish-eating species, such as larger bass, pickerel, gars, and others. Thus, the chances of survival of a new year-class of bass beyond the fry and small fingerling stages may be poor if a lake already contains a large population of yearling bass (13–18 cm) ready to prey upon them. Actually, with

Fig. 10. — Fishermen angling for bluegills in deep water using night crawlers or catalpa worms (larvae of the catalpa sphinx moth) for bait. The distance from the boat to the pier is about 35 meters.

a large yearling bass population already present, there is little need for a strong new year-class to maintain a high population and replace bass caught by angling.

Unfortunately, in planning a drawdown for a specific lake it is impractical to apply "cookbook" methods. Adequate sampling should indicate the level of overpopulation and stunting, and the severity of the drawdown should vary directly with the severity of stunting. If overpopulation were the only consideration, the situation still might be fairly simple. However, lake habitats vary in amounts of protective cover, and basin contours differ to such an extent that a drawdown designed to give a selected surface area reduction in one lake may not produce a comparable surface area reduction in another. The knowledge of how to use the drawdown as a management tool in a specific lake must come through trials and appraisals of their effects. Lantz *et al.* (1967) and Hulsey (1959) mention an additional value of drawdowns in controlling potamogetons and naiads. However, drawdowns may be responsible for increasing vegetation of certain kinds, such as *Potamogeton crispus* L., which may be given an opportunity to get started in deeper water while the lake level is down.

Whether a drawdown should be made every year is still an open question and probably depends upon the severity of the stunting problem prior to the preliminary test. At Ridge Lake 2 successive years of severe drawdowns were believed to have reduced the population more than was necessary (Tables 1 and 3, 1953 census). Perhaps the lesser drawdowns of 1953–1955 would have improved the bluegill population more than they did if they had been started in 1951 and carried through 1955 without the 1953 draining census. It is evident that testing the drawdown technique is a promising field for a great deal of additional research.

The period of stable water levels that extended from April 1956 to the draining census of October 1959 constituted a period of "no management" of the fish population. During this period the bass population reached a weight low (except for the census of 1953 after 2 successive years of severe drawdowns), and the bluegills reached a numerical high of 13,469 per hectare (Table 3) and a weight high second only to that of 1947.

As mentioned above, bluegill numbers were curtailed by drawdowns and biennial cullings. The latter gave the bluegills two growing seasons to make a comeback (Table 13), and the maximum weight buildup for these 2-year periods occurred in 1945 and 1946, with 9,152 individuals per hectare exposed in the 1947 census. Stable water levels actually existed in the four growing seasons of 1956–1959, terminated by the fall census of October 1959, and in the three growing seasons of 1960–1962, terminated by the spring draining census of March 1963. The bluegill population was numerically larger in 1963 after 3 years without drainings or drawdowns (Table 13) than it had been in any of the 10 previous 2-year periods between drainings, 1941–1951, and was even larger in 1959 after four seasons without drainings or drawdowns than it had been after three such seasons. While these data are not conclusive, they suggest that the bluegills in Ridge Lake, if left alone, would constantly increase in numbers until within a relatively short time the lake would become overpopulated with a stunted population of these fish.

As described in the section on the stable water period, the test of the usefulness of hybrid sunfishes in Ridge Lake was invalidated when the lake was contaminated by bluegills and warmouths, the parent types of the bluegill x warmouth hybrids being tested. Neither of these two pure species appeared in the creel census of 1960, but a few bluegills were observed in the lake in 1960 and a few of both species were caught by fishermen in 1961 (Table 19). Both species were common during the summers of 1961 and 1962, but the original source of these fishes is unknown.

So that Ridge Lake fishermen could legally keep only the largest hybrids, we placed a minimum length limit of 17.5 cm on these fishes. In 1960 fishermen caught 3,772 of the 4,503 hybrids that had been stocked in April, returning 3,708 and keeping 64. In 1961, after 448 additional hybrids (red-ear x warmouth) had been added in May, fishermen caught 4,890 hybrids, keeping 194 bluegill x warmouth and 6 red-ear x warmouth hybrids and returning 4,690. Because the fishermen could not with certainty or did not separate the two kinds of hybrids among the fishes released, it was impossible to compute the ratio of the two kinds in the catch.

In 1962 all length restrictions on the hybrids were removed, and fishermen caught and kept 1,075 bluegill x warmouth and 134 red-ear x warmouth hybrids. After the 1962 fishing season when hybrids of any length could be taken, the population remaining to be exposed in the 1963 spring draining census consisted of only 8 bluegill x warmouth and 64 red-ear x warmouth hybrids.

The small numbers of hybrid sunfishes in the anglers' catch of 1962 and in the spring draining census of 1963 suggest that many of these hybrids died as a result of hooking injuries sustained in being caught and released. This hybrid study was reported in a junior author's recent publication on hybrid sunfishes (Childers 1967:189). The hybrid sunfishes in Ridge Lake showed biting characteristics similar to those of hybrid sunfishes in other tests, i.e., they were highly aggressive and bold in taking fishing baits and were very easily caught. It was estimated that in 1962 at Ridge Lake 65 percent of the 1,209 hybrid sunfishes were caught in the first 5 days of fishing and 81 percent were caught in the first 10 days.

The catch of largemouth bass during the hybrid sunfishes period, 1960–1962, inclusive, was the poorest of any period between draining censuses (Table 19). This poor catch may have been influenced by two factors: (i) the small number and poor physical condition of the bass returned to Ridge Lake after spending the winter of 1959–1960 in a hatchery pond (which probably slowed the rebuilding of the bass population) and (ii) the introduction in 1960 of 585 lake chubsuckers into the lake (which may have increased the bass food supply and made them less vulnerable to angling). In 1960 the estimated number of bass fry was 3,050 per hectare (Table 10). This fry population could have been the origin of a large new year-class of bass. In 1961 no schools of young were seen, and in 1962 only one school was observed. Yet, in the 1963 draining census we found the numerically largest bass population exposed in any census (Table 1), 6,218 bass, of which 6,042 ranged in size from 12.7 to 25 cm and were quite obviously members of the 1962 year-class. A comparatively small number of larger bass (176) was also present, of which 86 were fin clipped from previous censuses. Of the 299 bass moved back to the lake in 1960, 44 were caught in 1960, 48 in 1961, and 15 in 1962, a total of 107 of the 299. Eighty-six marked bass were taken in the 1963 draining census, and only 62 bass representing the 1960 and 1961 year-classes were present. Fishermen had caught 156 bass of these same year-classes in 1961 and 1962. These figures indicate that the bass population was characterized by low production and survival rates in 1960 and 1961. Only in 1962 was there an unusually high survival of a relatively small spawn. It therefore seems reasonable that, at least prior to 1962, the presence of a dynamic population of lake chubsuckers had little effect on the bass population or on bass fishing although from 1960 to 1963 the chubsuckers increased from 585 to 3,182.

One of the most interesting points to

come from the study of the fishes of Ridge Lake was the capacity of the largemouth bass and bluegills to expand their populations when their numbers were decimated by artificial culling such as was done in the biennial draining period 1941–1951 and every time we drained the lake thereafter. One might assume from the way these populations recovered that such adversity was common and that these fishes had evolved under environmental catastrophies that produced severe stresses. Even what might appear to be abnormal losses of larger bass through angling—56–63 percent of the available numbers of marked bass per fishing season (Table 17)—were quickly replaced through recruitment and growth.

In contrast, stable water levels and insufficient culling (i.e., protection of small fishes) eventually resulted in less desirable fish populations, at least from the standpoint of numbers of large fishes available for angling. This fact indicates that there is a great deal of room for improvement in fish management to provide better fish populations for angling. But such a potential for improvement cannot become a reality until anglers and fish managers modify much of their present thinking.

SUMMARY

1. — Ridge Lake was stocked with 335 yearling largemouth bass and 100 adults in 1941, 129 bluegills in 1944, 138 warmouths in 1949, and varying numbers of channel catfish in 1951, 1952, and 1957. After an attempt to remove all bluegills by draining the lake and leaving the lake basin empty over the winter of 1959–1960, 585 lake chubsuckers and 4,500 hybrid sunfishes were stocked in the spring of 1960.

Since the beginning of this study in 1941, 29,700 largemouth bass, 390,000 bluegills, and about 10,000 warmouths have been permanently removed from the lake. The lake now (1968) contains adequate numbers of all species stocked except channel catfish, which did not reproduce successfully in standing water.

2. — A complete creel census has been conducted at Ridge Lake each summer except in 1941 and 1943, when the lake was closed to public fishing. In addition, the lake was drained and the fishes were censused in the springs of 1943, 1945, 1947, 1949, 1951, 1953, 1956, 1959 (fall), and 1963, and selected kinds, sizes, and numbers of fish were held alive and restocked (Tables 1–4).

3. — In the nine draining censuses at Ridge Lake bass total numbers varied between 1,500 and 6,000 and their total weights between 205 and 412 kg (Table 1). Bluegill total numbers ranged from 7,500 to 93,000 and their weights from nearly 450 to about 1,580 kg. Warmouth populations varied but were always small. The total weight of channel catfish varied with the number present; a few grew to more than 4.5 kg each. Lake chubsuckers were stocked in 1960. Other fishes in the lake probably came from the watershed and were mainly green sunfish, black bullheads, yellow bullheads, carp, and minnows. These never made up more than a small part of the population.

4. — Standing crops of largemouth bass varied between 35 and 56.6 kg per hectare (Table 3). In four censuses the standing crops of bass approached or slightly exceeded 56 kg per hectare, suggesting that this weight may represent the maximum this lake will support. There was no increase in the standing crop of bass when bluegills were present over that of bass by themselves. Standing crops of bluegills varied from 65.3 to 216.7 kg per hectare. There was no suggestion of a maximum standing crop of bluegills. The standing crop of warmouths never made up more than 5 percent of the total number or weight of any fish population exposed in a draining census.

5. — When substantial numbers of both bass and bluegills were present (Table 3), the standing crops of all fish

in the censuses of Ridge Lake varied between 157.2 and 287.4 kg per hectare. Usually when bass weight increased, bluegill weight decreased, and vice versa.

6. — Biennial lake draining with the culling of small bass and bluegills increased the numbers of large bass and was selective for fast growing ones, i.e., bass that did not attain lengths of 20–25 cm in two growing seasons were permanently removed from the lake.

7. — Early fall drawdowns drastically reduced the numbers of small bluegills and allowed an increase in the numbers of large ones because of increased growth rate (Table 9). Drawdowns maintained large numbers of small bass but did not increase the numbers of large ones (Table 7). The reasons for reduced populations of large bass are unknown.

8. — Four growing seasons without lake drainings or drawdowns resulted in the production of a large numerical population of bluegills and a small population of largemouth bass (Tables 1 and 3).

9. — Hybrid sunfishes were more easily caught than the pure parent species, but offered little competition to the parent species in Ridge Lake.

10. — Bass fry production after a draining and culling of small fishes of all kinds averaged 7,917 per hectare; after drawdowns, 3,243 per hectare; and after 1 or more years of stable water levels, 1,023 per hectare (Table 10).

11. — The ratios between estimated numbers of bass fry produced in census years during the 10-year period of biennial drainings and censusings and the number of yearlings of the same year-class caught by fishermen or appearing in the next census 21 months later varied from 29 to 1 (greatest survival rate) to 196 to 1 (lowest survival rate) (Table 11). Probably all of these ratios were abnormal, as during postcensus summers the numbers of bass fry predators, such as small fishes and predacious aquatic invertebrates, were much reduced.

12. — There was no relationship or a negative relationship between the estimated numbers of bass spawners and the estimated numbers of fry produced (Table 12). However, there appeared to be a definite negative relationship between large numbers of small bluegills and numbers of bass fry. In 1946, 1948, and 1950 when 2,500 or more small bluegills per hectare were present, bass fry survival was negligible (Table 12).

13. — Expansion of the bluegill population in Ridge Lake was positively related to time and negatively related to drawdowns and to "dominant" populations of bass (Table 13). However, bass were unable to control bluegills completely except when given the assistance of fall drawdowns.

14. — One largemouth bass belonging to the 1941 year-class and marked in 1943 was taken for the last time in the census of 1956. A few other marked bass lived for 10, 11, and 13 years, but most marked bass disappeared at ages 7–10 years.

Seasonal exploitation rates from catches of marked largemouth bass ranged from 1.5 to 63 percent (Table 14). But even with the higher exploitation rates there was no evidence of overfishing, and replacement rates were increased through recruitment and accelerated growth rates.

15. — Natural, nonfishing mortality for largemouth bass at Ridge Lake (figured for 2-year periods) was 33 percent for bass weighing 0.07–0.34 kg, about 14 percent for sizes between 0.35 and 1.81 kg, 39 percent for sizes between 1.82 and 2.27 kg, and 73 percent for sizes over 2.27 kg (Table 16).

16. — The nine draining censuses with the culling of small fish and invertebrate fish foods influenced the hook-and-line catch in the postcensus angling seasons to the extent that yields averaged 55.9 percent of the bass available (representing 62.6 percent of their weight) (Table 17), while in precensus fishing seasons, not influenced by culling, an average of 60.3 percent of the number of bass available (representing 39.2 percent of

their total weight) were captured (Table 18). Comparable averages for bluegills for postcensus seasons were 38.1 percent (representing 49.1 percent of weight) and for precensus seasons 49.7 percent (representing 46.0 percent of the total weight of bluegills).

17. — Fishing pressures (from boats only; no bank fishing) at Ridge Lake varied from 222 man-hours to 791 man-hours per hectare per season (Table 20). Average seasonal rates of catch ranged from 0.1 to 1.8 fish per man-hour; these catches represented average seasonal rates of 7–34 hours to catch 1 kg of fish. These averages include all of the unproductive time spent in fishing by fishermen who caught nothing as well as productive time spent by those who caught fish.

18. — Rates of catch varied so that seasonal fish yields ranged from 3.3 to 117.0 kg per hectare, giving an average for 21 years of 47.7 kg per hectare (Table 23). Five to 10 times as many fishes were caught in good fishing years as in poor ones.

19. — In 3 poor fishing years the average number of large bass present per hectare was 59, and small ones averaged 123, a total of 182 per hectare. For bluegills the average number of large fish per hectare was 175, and small bluegills averaged 194, a total of 369 per hectare (Tables 28 and 30). In 3 good fishing years the average number of large bass present per hectare was 73; the number of small, 158; the total 231 per hectare. For bluegills the average number of large fish per hectare was 1,315; the number of small, 1,103; the total, 2,418 per hectare (Tables 29 and 30). Numbers (and weights) of fish were the most important differences between good and poor fishing years. The competition, presumably for the available food, produced by large numbers of fishes made fishing returns greater when populations were larger.

20. — The average annual catch of desirable-sized largemouth bass (25 cm or longer) per hectare was 47, weighing 19.2 kg, under biennial draining and culling; 30 per hectare, weighing 11.7 kg, under drawdowns; and 27 per hectare, weighing 12.1 kg, under stable water levels. For desirable-sized bluegills (15 cm or larger) the average annual catch per hectare was 133, weighing 13.0 kg, under biennial culling; 304 per hectare, weighing 33.2 kg, under drawdowns; and 472 per hectare, weighing 41.9 kg, under stable water levels (Table 31).

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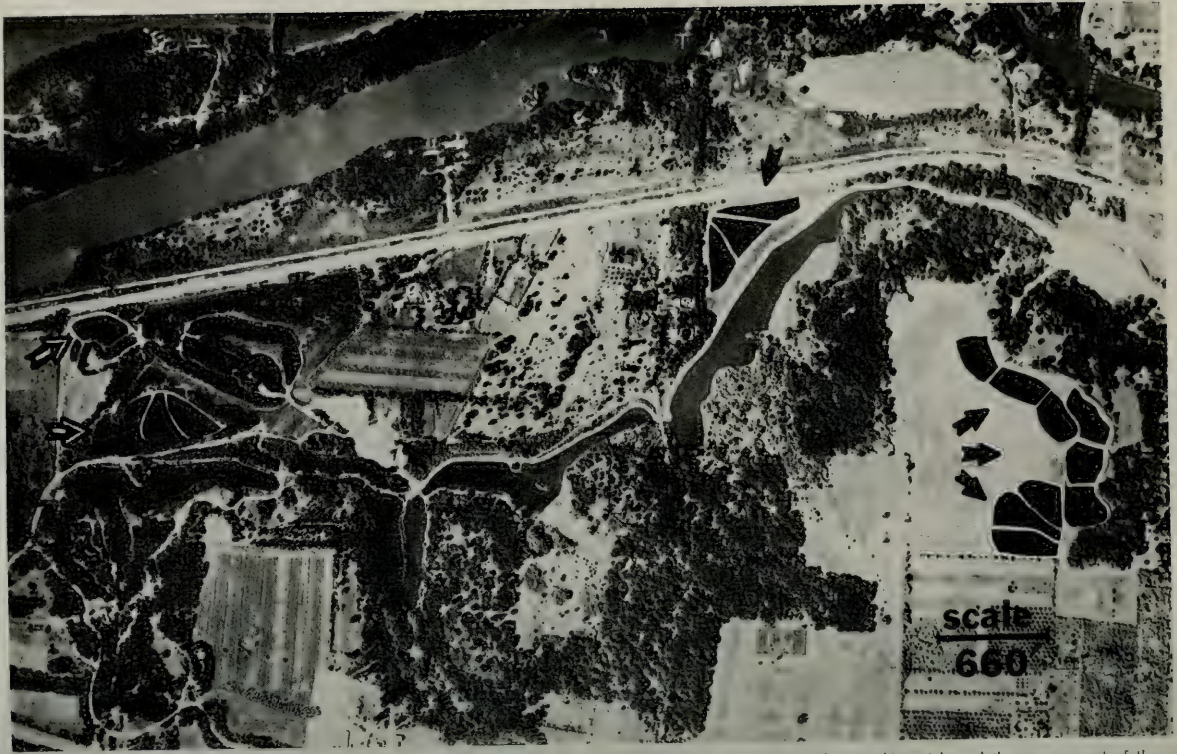

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Dynamics of One-Species Populations of Fishes in Ponds Subjected to Cropping and Additional Stocking

D. Homer Buck
Charles F. Thoits III

THIS REPORT is based on several years of intensive studies of the production and related population dynamics of six kinds of warmwater fishes maintained as single species in 1-acre ponds. Species involved included the largemouth bass, *Micropterus salmoides* (Lacépède); smallmouth bass, *M. dolomieui* Lacépède; bluegill, *Lepomis macrochirus* Rafinesque; yellow perch, *Perca flavescens* (Mitchill); brown bullhead, *Ictalurus nebulosus* (LeSueur); and the white crappie, *Pomoxis annularis* Rafinesque. Most production data published for these species have originated primarily from studies involving complex, multispecies populations. Only Bennett & Childers (1957), Cooper *et al.* (1963), and Eipper (1964) are known to have made comprehensive studies of the dynamics of populations having only a single species.

The principal aims of this investigation were to 1) increase our knowledge of the carrying capacities of ponds for warmwater fishes, 2) consider the relationship of carrying capacity to standing crop and to rate of production, and 3) measure the influence of controlled population increases and decreases on fish production.

It was assumed that physically similar, contiguous ponds would have reasonably similar characteristics and/or production potentials, and that differences in production could be related to treatments administered. Thus, emphasis was placed on the collection of fish population data, as opposed to intensive environmental analyses.

An attempt was made in these investigations to determine how nearly standing crops approximated carrying capacities. Although the data provided clear indications in some instances, we were dealing with a complex relationship that merits some preliminary examination.

The evolution of the carrying capacity concept has been quite thoroughly treated by Edwards & Fowle (1955). Somewhat later, Krumholz *et al.* (1957) reviewed the status of wildlife terminology and proposed the following definition of carrying capacity as one widely applicable to both fish and game biology: "the maximum number (or weight) of organisms of a given species and quality which can survive in a given ecosystem through the least favorable environmental conditions that occur within a stated interval of time." These writers further observed that in general the most appropriate "stated interval of time" is one year. By the terms of this definition, carrying capacity involves a minimum quantity which places limitations upon its practical application. If the interval of time is a year, the carrying capacity becomes the minimum population present during the annual cycle. Frequently, however, it is of more value to determine maximum rather than minimum rates of abundance. Only maximum rates, for example, permit the proper evaluation of the harvestable crop, or of the comparative production potentials of two species or combinations of species, or permit the proper evaluation of a remedial treatment in fisheries management. It would therefore seem desirable to measure carrying capacities at seasons other than when conditions for survival are poorest.

A more useful concept might therefore be that of Bennett (1962:59), who proposed the following definition of carrying capacity as one applicable for fishes: "the maximum poundage of a given species or complex of species of fishes that a limited and specific aquatic habitat may support during a stated interval of time." In eliminating the restrictive clause "through the least favorable environmental conditions," Bennett effectively removed the requirement for a minimum quantity, and in this respect his definition resembles the "current carrying capacity" of Edwards & Fowle (1955). One then becomes free to evaluate carrying capacity at any season for which suitable data may be obtained.

The question logically arises as to why standing crop may not in itself provide a satisfactory measure of carrying capacity, or of potential rates of abundance. It may, of course, at times. It is widely recognized, however, that the two are not necessarily the same, and that standing crop might be lower than, equal to, or in excess of the carrying capacity (Krumholz 1948, Bennett 1962, and others) due to changes in habitat, food supply, or population structure.

Carrying capacity is often conceived to be a relatively stable quantity, changing little from year to year. Theoretically, under comparatively stable conditions such as an extremely sterile lake or an extremely fertile, continuously fertilized pond, the carrying capacity could conceivably be quite stable. In the first instance one or more factors would be definitely and continuously deficient, or limiting, so that production would be at a continuously low level, as in a northern oligotrophic lake. In the second instance the essential nutrients would be supplied in a continuous abundance so that production might tend to remain near its potential maximum. Such a condition might be found in a southeastern pond so fertilized that available nutrients were channelled directly into the production of a continuous abundance of phytoplankton, zooplankton, and tertiary feeders with none diverted into the growing of higher plants. In both instances the flow of energy would tend to follow a reasonably regular and direct path. Between these two extremes exist those intermediately productive, unfertilized waters where the factors influencing production may exist in an almost infinite variety of combinations and the flow of energy may be channelled through a great variety of paths. The ponds of the present study typify such an intermediate category.

References made to carrying capacity in this paper are intended to represent the current or temporary carrying capacity which existed at the time of observation and may not necessarily represent the carrying capacity at the time when conditions for survival were poorest.

The investigations were conducted at the former McGraw Hydrobiological Laboratory near Dundee, Ill. Limited investigations were begun in 1956, but the majority of the data were collected in the years 1958-1963. The project was designed to continue for a minimum of 15 years as a cooperative program of the North American Wildlife Foundation, The Illinois Department of Conservation, the Illinois Natural History Survey, and the McGraw Foundation. As a result of organizational changes within the McGraw Foundation, the program was prematurely terminated in November 1963.

ACKNOWLEDGMENTS

The investigations were centered in 16 1-acre ponds constructed especially for this study. Pond construction was financed in part and an office and laboratory work space were provided by the North American Wildlife Foundation. Additional financial support for pond construction and other items of use in the program was provided by the Illinois Department of Conservation, and for the period 1956 through October 1961, that agency assigned to the project a full-time biologist. From

October, 1961, partial financial support was received through the Dingell-Johnson program, including salary and expenses for the assistant leader. Planning and administration of the program, financial support for the program leader, summer field assistance, and major equipment support was provided by the Illinois Natural History Survey throughout the course of the investigations.

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For assistance with summer field work, we are grateful to Robert M. Eichler and Warren U. Brigham.

The program was conceived and designed by Dr. George W. Bennett, and we gratefully acknowledge his suggestions and encouragement throughout the investigations as well as his critical review of the manuscript. We are additionally grateful to O. F. Glissendorf for his editing of the final manuscript, and to Richard M. Sheets for drawing the figures.

DESCRIPTION OF THE AREA AND PONDS

The study area, in Kane County, Illinois, is approximately 35 miles south of the Wisconsin state line, and 30 miles west of Lake Michigan. It lies within the Wisconsin glaciation, with a rolling topography formed by the irregular deposition of glacial material. Major relief occurs only along waterways. The land is fertile and intensively devoted to the culture of corn and soybeans. Physiography and characteristics of the soils have been presented by Hopkins *et al.* (1917), and the climate of the area is described by the Atlas of Illinois Resources (1958).

The study ponds were located within a block of approximately 1,200 acres operated as a hunting and fishing club. This was an area of irregular topography, lying partly on high ground overlooking the Fox River to the west and dropping rather abruptly to the floodplain from points as high as 170 feet above the river. Steeper slopes were heavily wooded with native hardwoods and cut by frequent natural drainage ways to the river. Within this area were two series of club fishing lakes at two distinct levels. These contained mixed populations of warmwater sport fishes and were the source of water for most of our experiments. The only exceptions were three ponds used in our first series of smallmouth bass experiments which were filled by a partial diversion of an artificial spring-fed trout stream.

The major system of 15 ponds was constructed in five units, each containing three contiguous ponds. Because of differences in location, in types of bottom materials, and in age, or completion dates, the ponds presented a rather wide range of characteristics. Table 1 presents the names, dates of completion, and various chemical and physical characteristics of the ponds in each of the five units, plus the single pond Alpha.

All ponds were designed to have a surface area of 1 acre and a maximum depth of 8 feet, with average depths of between 3 and 5 feet. Pond banks were steep in slope (approximately 1:1) to minimize growth of shoreline plants. Grade of pond bottoms was established to provide 1 foot of rise in the first 50 feet from the drain, and 1 foot additional rise for each 100 feet thereafter. Pond shapes varied from approximately round to an irregular L-shape, depending upon topography, but the most common shape was triangular — wide at the shallow end, and forming a narrow apex at the drain (Fig. 1).

Table I.—Some physical and chemical data from ponds built on the property of the McGraw Foundation near Dundee, Illinois and used for carrying capacity experiments. When filled, each pond had a surface area of 1 acre.

Unit	*Pond*	*Year of Completion*	*Bottom Material*	*Relative Fertility*	*Average pH*[a]	*pH Range*	*Average Total Alkalinity*[a]	*Average Transparency, Inches (Secchi disc)*[a]	*Submersed Aquatic Vegetation*
1	Alpha	1956	Black Dirt, Clay, & Gravel	Medium	8.6	8.5–8.7[b]	203	50.4	None[c]
	Beta	1957	"	High	8.9	8.3–9.9	199	72.5	Abundant[d]
	Gamma	"	"	"	8.7	8.3–9.0	180	83.6	"
	Delta	"	"	"	9.2	8.0–10.2	188	60.2	"
2	Zeta	1958	Sand & Clay	Low-Medium	8.8	8.6–9.0	161	41.6	Moderate
	Theta	"	"	"	9.4	9.0–9.8	117	44.0	"
	Iota	"	"	"	9.2	8.7–9.9	149	35.8	"
3	Kappa	"	Clay	Low	8.7	8.0–9.2	148	16.7	Scarce
	Lambda	"	"	"	9.2	8.7–10.2	113	22.0	"
	Rho	"	"	"	8.9	8.6–9.4	145	22.5	"
4	Sigma	"	"	"	8.9	8.6–9.4	134	26.0	"
	Tau	"	"	"	9.1	8.6–10.1	105	36.0	"
	Upsilon	"	"	"	9.1	8.4–9.8	106	32.0	"
5	Phi	1960	"	"	8.8	8.4–9.7	91	22.4	None
	Chi	"	"	"	8.7	8.0–9.2	93	15.2	"
	Psi	"	"	"	8.7	8.5–9.2	118	20.1	"

[a] Average alkalinities and pH and Secchi disc readings were based on weekly determinations, usually made between 9 A.M. and noon, throughout the 1962 growing season.
[b] In 1961, with abundant vegetation, pH in this pond exceeded 10.2 and caused total loss of a chain pickerel population. With no vegetation in 1962, pH remained low.
[c] Although weedless in 1962, this pond contained abundant stonewort (*Chara*) in other years.
[d] Beta, Gamma, and Delta were extremely variable, with weeds ranging from abundant to none in various years.

Descriptive data listed in Table 1 are generally self-explanatory, but two items deserve comment. Daytime pH values in most ponds ranged abnormally high. Since the testing apparatus used had an upper range of 10.2, the average pH, as well as the upper range, could have been higher in these ponds for which a high of 10.2 is listed. The high values were associated with intensive rates of photosynthesis, and consequent replacement of absorbed carbonate and bicarbonate ions by released hydroxyl ions. Such extremes are not uncommon in small ponds having poorly buffered waters (Ruttner 1953). High pH (10.2 or above) was credited with the deaths of an experimental population of chain pickerel, *Esox niger* LeSueur, at this station, and had some influence on the spawning of largemouth bass, as is discussed in a later section.

Density of submerged aquatic plants varied greatly from pond to pond, as well as from year to year, and was usually positively correlated with age, fertility, and clarity of the pond (Table 1). Weeds were not observed in Unit 5, were relatively scarce in Units 3 and 4, moderately abundant in Unit 2, and often extremely abundant in pond Alpha and in Unit 1. The most common forms were the curley-leaf pondweed, *Potamogeton crispus* L., and sago pondweed, *P. pectinatus* L.; almost as common was *P. foliosus* Raf. Less common were *Anacharis canadensis* (Michx.) and a bushy pondweed, probably *Najas flexilis* (Willd.). A water milfoil, *Myriophyllum exalbescens* Fernald was observed only in pond Theta, and horned pondweed, *Zannichellia palustris* L. only in pond Delta.

With the exception of pond Alpha, all ponds received at least one treatment of inorganic fertilizer. While each of the three ponds in a unit received equal treatments, those units thought to be the least fertile received additional amounts (Table 2).

Table 2. — Kinds and amounts of fertilizers used in the various pond units, and dates of application.

Fertilizer	*Pounds Per Acre*	*Pond Units Treated*	*Date*
0/20/0	100	1, 2, 3, 4	6/02/59
0/20/0	100	4	6/29/59
10/10/10	100	3, 4, 5	5/14/62
0/46/0	26	3, 4, 5	5/25/62
0/46/0	28	3, 4, 5	6/25/62
0/46/0	28	5	7/20/62

EXPERIMENTAL DESIGN AND METHOD OF OPERATION

The original plan of study involved the simultaneous operation of the 15 ponds, divided into five units of three ponds each, with each unit devoted to a single species of fish. The 15 populations were to be studied through three growing seasons, following which all ponds would be drained and censused and the population of each unit rotated into a new unit for a similar study. This was to be continued through five 3-year periods, or until each of the five species had been rotated through each of the five units of ponds.

Due to the staggered completion date of the ponds it was not possible to initiate the original plan until the total of 15 ponds became available in 1961. However, preliminary investigations were launched as the ponds became available and, when possible, these ponds were operated on a schedule similar to that originally planned. Where units of three ponds were available each pond was stocked with similar numbers and sizes of the same single species. One of these (the "cropped" pond) was then cropped at a predetermined rate from April through September, and the majority of those fish were marked and added to a second pond (the "add-stock" pond). The third pond in each unit (the "control" pond) was neither cropped nor "overstocked," and was left to develop naturally. All ponds were sampled at regular intervals to measure comparative fish growth and condition, and some fishable populations were subjected to limited hook-and-line fishing. The principal deviation of the pre-1961 experiments from the original design was in the interval of study. Final censuses were made after only one and one-half or two seasons, rather than after three growing seasons.

An additional part of the design was to drain and census the population in each "control" pond (one in each unit) at the end of the first growing season so that this early population development might be compared with that attained after longer periods. Additional spring and fall inventories were made by utilizing Petersen estimation procedures. Those few estimates which could be supported by supplementary draining censuses or other information have been utilized herein, but the majority of the estimates were believed to be too unreliable for presentation. In a study of these same populations, using seines for obtaining samples, we found that the Petersen procedures tended to provide a high proportion of gross underestimations (Buck & Thoits 1965).

In censusing the ponds, fishes and water were allowed to pass through the drains into a modified Wolf-type weir where the fish were trapped and transferred to holding tanks or live boxes. Data collected included individual lengths and weights of fish older than Age O, individual lengths and weights of an adequate sample of Age O fishes, length frequency distributions, and total weight of all fishes. All fishes were then resorted into equal numbers of various size or age groups and randomly restocked in a different unit of ponds. Other observations recorded at this time included kinds and relative amounts of aquatic vegetation, abundance of tadpoles and crayfish, and kinds and abundance of the more common aquatic insects. As a part of one draining operation the waters from three ponds were strained through a special filter which retained all stages and sizes of aquatic insects, scuds, and larger zooplankters, and permitted an estimate of standing crops of these invertebrate forms.

Prior to 1963 all fish populations were sampled at intervals of 2 weeks throughout most of the growing season (usually April through September). In 1963, samples were collected every third week. Most sampling was by use of a large seine, 185 feet long, 12 feet deep, and with ⅜-inch mesh. This was supplemented by sampling with smaller seines for small fish, wire traps for perch and bluegills, and hook-and-line fishing and a-c boat shocker for perch and smallmouth and largemouth bass. Only bullheads were collected exclusively by seining. Efforts were made to sample all age components of each population at each sampling period, with a sampling goal of at least 100 fish for each abundant age class. Whenever possible, sampling of an individual pond was accomplished in a single day. However, when samples were difficult to obtain, sampling of an individual pond often continued over several consecutive days. Fish were weighed and measured when caught, except that hook-and-line and boat shocker samples taken at night were usually not processed until the following morning. Cropping and the transfer of stock was integrated with sampling. Individual lengths and weights were taken of larger fish; smaller fish of uniform sizes were often weighed in groups of 10 or 20.

In this study index of condition (C) was arrived at by employing the method of Thompson & Bennett (1939) using the formula

$$C = \frac{10{,}000\ W}{L^3}.$$

Various fin clips were used to indicate the age of fishes, to designate those being transferred, and to indicate the season of transfer. If a fish to be stocked at the beginning of a new experiment bore no previous age mark, census mark (including that of the first-year census of a control pond), or sampling mark, it was given a fin clip indicating its approximate age. Because of frequent spawning failures, year classes were in many cases easily distinguishable by size. This fortunately was true for the bluegill population where age distinctions would have been the most difficult. Even when consecutive year classes were produced there were periods when age separations were possible and unmarked fish could be marked, thereby defining the range of sizes for the several year classes in later draining censuses. All individuals in some year classes were marked, and in most cases a majority of individuals in each class had received an identifying mark by the time of the final census. The major exception was in the largemouth bass where cannibalism was responsible for considerable overlapping of age classes before the fish could be marked. In these instances the censused populations were divided into size classes, which to a large extent approximated age classes.

Mortalities from marking were generally quite negligible. Also, most clips were found to be permanent. When partially regenerated fins were encountered in sampling, the regenerated portions were removed. Fish with completely regenerated fins were identifiable by malformations of the fin.

PRESENTATION OF DATA

The data are presented by individual species. Primary subjects considered include growth, condition, reproduction and survival rates, mortality rates, and the influence of the experimental stocking and cropping on production. Included are standing crop totals, along with supplementary data, for 11 populations of smallmouth bass, 10 of largemouth bass, 6 each for yellow perch and white crappie, and 4 each for bluegills and brown bullheads. Supplementary data include number of growing seasons, pounds originally stocked, pounds added or pounds cropped, and pounds lost or gained over the course of the experiment.

The pounds lost or gained figure is intended to represent the weight of fish produced in the pond, less natural mortality. Thus, from the standing crop figure we subtracted pounds originally stocked, and pounds added, then added pounds cropped, to derive the sum of pounds lost or gained. This final summation is identical with Ricker's (1958) surplus production when computed for a single season, when no stock was added during the season, and when the poundage present at the start of the season approximated carrying capacity. It differed from Ricker's statistic when original stock was below carrying capacity, when stock was added to the population, or when computed for a period longer than one calendar year. Where applicable, our figure of pounds lost or gained is used interchangeably with Ricker's surplus production. This statistic provides a useful measure of production, and permits an evaluation of the influence of the population manipulations involved and how nearly the standing crops attained, or whether they exceeded, the carrying capacities of the ponds at the times of census.

SMALLMOUTH BASS

The stock of smallmouth bass used in these studies was obtained from small ponds located on the grounds of the former Fin 'n Feather Club, near Dundee, Illinois, where they had been maintained in club fishing ponds for a number of years. The source of the club's stock is not known. Smallmouth stocked in pond Alpha in July, 1956, spawned the following spring, and progeny from this stock were used in all subsequent experiments.

Pond Alpha was completed and first filled with water in July, 1956, and was stocked with 16.2 pounds of smallmouth consisting of 95 sub-adults (mostly Age I) in July of that year. Ponds in Unit 1 (Beta, Gamma and Delta) were completed and first filled in May, 1957, but were first stocked with smallmouth in May, 1958. On May 13, each pond received a total of 5.6 pounds of smallmouth consisting of 10 adults averaging 9.8 inches total length, and 40 fingerlings (Age I) averaging 4 inches total length. Adults were observed to spawn in all three ponds in the first week following their release. These ponds were drained and censused in October, 1959, following two seasons of growth.

Following the 1959 censuses, age groups of smallmouth from all ponds were combined and randomly restocked in equal numbers of the several size (age) groups in each of the same three ponds. Total weights of these new populations were between 90 and 97 pounds. The ponds were drained and censused in October, 1960, following the single season of growth.

Ponds in Unit 4 (Sigma, Tau and Upsilon) had been completed in August, 1958, but were not available for the smallmouth experiment until 1960. Thus, the ponds were slightly over 2 years old when first stocked with smallmouth bass in October of 1960. Unit 1 was the source of fish for Unit 4. Stockings were heavy, being approximately 130 pounds per acre in each pond, composed principally (about 92 percent by weight) of Age II fish (1958 year-class). From a review of available information collected during the winter of 1960-1961, it was decided that the fall stocking of Age II fish had been excessive. Accordingly, in mid-April, 1961, 60 of the dominant age class (now Age III) were removed from ponds Sigma and Upsilon, and 59 were removed from Tau. Total weights of these fish were 20.93, 21.79 and 21.45 pounds from ponds Sigma, Tau and Upsilon, respectively. It was believed that these reductions might improve the food-feeder relationships between the food producing potential of the ponds and the bass populations. Additional population adjustments and transfers of stock are presented in subsequent text and tables.

Standing Crop Data

Table 3 presents standing crops in pounds per acre for 11 populations of smallmouth bass arranged according to experimental treatments given the populations, with an average standing crop presented for those ponds receiving

Table 3. — Standing crops in pounds per acre of smallmouth bass in ponds receiving different experimental treatments. All censuses were by pond drainage and count of fishes at the ends of the growing seasons.

Unit	*Pond*	*Number of Growing Seasons*	*Year of Census*	*Standing Crop in Pounds Per Acre by Treatment Received*		
				Control	Cropped	Add-stock
..	Alpha[a]	1½	1957	64.7	..	..
1	Delta	2	1959	26.4	..	..
1	Gamma	2	1959	..	73.0	..
1	Beta	2	1959	..	..	180.0
1	Beta	1	1960	169.0	..	..
1	Delta	1	1960	..	56.3	..
1	Gamma	1	1960	..	..	173.4
4	Sigma	1	1961	84.9	..	..
4	Sigma	2	1963	93.2	..	..
4	Tau	3	1963	..	9.3	..
4	Upsilon	3	1963	..	..	95.5
			Average	*87.6*	*46.2*	*149.6*

[a] Operation of this single pond was similar to that of the regular control ponds, and it is so classified here.

identical treatments. Table 4 shows the same standing crop data together with such pertinent supplementary data as pounds originally stocked, pounds added to or removed from the populations during the course of the experiments, and the net loss or gain in pounds of fish flesh by the termination of the experiment. All censuses presented in Tables 3 and 4 were by pond drainage with counts of all fishes at the ends of the growing seasons. Table 5 presents those standing crops obtained by estimation procedures in the spring, in addition to those obtained by draining censuses in the fall, for ponds Sigma, Tau, and Upsilon. Original stock, computations of pounds gained or lost, and other supplementary data in Table 5 were derived or computed from figures obtained from the previous census, whether it was by estimation or actual count.

Standing crops ranged from a high of 180 pounds per acre in the add-stock pond Beta in 1959 to a low of 9.3 pounds in grossly overcropped pond Tau in 1963 (Tables 3 and 4). Some of the known factors that contributed to these variations included 1) differences in experimental treatments received, 2)

Table 4. — Pounds of smallmouth bass per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Alpha, Beta, Gamma, Delta, Sigma, Tau, and Upsilon for periods of 1, 1½ (Alpha), 2 and 3 years. All censuses were by pond drainage and count of fishes at the ends of the growing seasons.

Unit	*Pond*	*Treatment*	*Year of Census*	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
..	Alpha	None	1957	1½	16.2	64.7	0.0	0.0	+48.5
1	Delta	Control	1959	2	5.6	26.4	0.0	2.5	+23.3
1	Gamma	Cropped	1959	2	5.6	73.0	0.0	69.8	+137.2
1	Beta	Add-stock	1959	2	5.6	180.0	41.7	1.1	+133.8
1	Beta	Control	1960	1	89.7	169.0	0.0	1.6	+80.9
1	Delta	Cropped	1960	1	97.4	56.3	0.0	86.2	+45.1
1	Gamma	Add-stock	1960	1	91.1	173.4	50.2	8.4	+40.5
4	Sigma	Control	1961	1	130.8	84.9	0.0	36.1	—9.8
4	Sigma	Control	1963	2	83.8	93.2	8.1	51.1	+52.4
4	Tau	Cropped	1963	3	133.1	9.3	5.5	126.9	—2.4
4	Upsilon	Add-stock	1963	3	129.6	95.5	84.9	50.8	—68.2

Table 5. — Standing crops of smallmouth bass in 1-acre ponds Sigma, Tau, and Upsilon, and pertinent supplementary data, from censuses in both spring and fall, by either drainage (exact count) or Petersen estimation procedures.

Pond	*Season and Year of Census*[a]	*Type of Census*	*Number of Growing Seasons*	*Standing Crop, Pounds Per Acre*	*Pounds of Original Stock*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
Sigma	F 1961	Drainage	1	84.9	130.8	0.0	36.1	—9.8
Sigma	S 1963	Estimate	2	56.4	83.8	8.1	50.5	+14.9
Sigma	F 1963	Drainage	1	93.2	56.4	0.0	0.6	+37.4
Tau	S 1963	Estimate	2	5.6	133.1	5.5	119.4	—13.6
Tau	F 1963	Drainage	1	9.3	5.6	0.5	7.5	+10.8
Upsilon	S 1962	Estimate	1	55.4	129.6	42.3	33.6	—82.8
Upsilon	S 1963	Estimate	1	64.5	55.4	36.5	15.8	—11.6
Upsilon	F 1963	Drainage	1	95.5	64.5	6.1	1.3	+26.2

[a] Symbols: F = fall, S = spring.

differences in pond fertilities and consequent differences in production of foods, and 3) differences in size and/or age composition of the populations. Except for the unusually low production in pond Delta in 1959, standing crops among contiguous ponds within the same experimental units were universally highest in the ponds which received additions of stock, lowest in those from which fish were cropped, and intermediate in those ponds which were maintained as controls.

Fertilities of the three ponds in Unit 4 were thought to be very similar, but ponds in Unit 1 exhibited rather marked differences in their productivities. These differences were believed to be related to the way these ponds were supplied with water while they were occupied by smallmouth. During this period the ponds were watered by partial diversion of the artificial, spring-fed trout stream mentioned earlier. The diverted water first entered pond Beta, from which it overflowed through a tube into the second pond, Gamma, and from which it again overflowed to fill the third pond, Delta. In addition, a small stream of water flowed into Beta for extended periods to make up losses through seepage and evaporation in all three ponds. Beta's productivity was probably enhanced by a greater water exchange, by an influx of drift organisms from the feeding stream, and from receiving nutrients not passed along in equal quantities to its companion ponds. The data indicated that productivity of smallmouth decreased in the order that the water filled and passed through the ponds, from Beta to Gamma to Delta. We thus may have experienced a progressive drain of both food and nutrients so that water reaching the last pond Delta was relatively sterile.

The rather wide range of differences in standing crops recorded in Table 3 merits additional discussion. The final standing crop of 64.7 pounds per acre in pond Alpha may have been short of the carrying capacity of this pond because 1) initial stocking was light (16.2 pounds) and little more than one effective growing season was involved, 2) the population contained only two year-classes, and 3) much larger standing crops were recovered from other ponds, including those believed to be less fertile, when more time was involved or initial stocking was larger.

The extremely low standing crop of 26.4 pounds of bass found in Delta in October, 1959, was due to a combination of low fertility, when compared with its two companion ponds, and to the virtual absence of the age classes O and I. No young could be found in Delta in 1958, and numbers of young bass were extremely limited in 1959. Weight gains of the population consisted almost entirely of flesh added to the original stock, which, at the time of census, included only 32 individuals. The absence of fish of Ages O and I was particularly critical in this instance since they comprised the greatest weight in both companion ponds. However, as the age and size distribution of fish in the three ponds was equalized at the time the ponds were restocked in November, 1959, the comparatively low standing crop in Delta in 1960 was believed to have been due to low productivity. Poor production in this pond in 1960 was evidenced by its low figure of "pounds gained" (45.1 pounds) (Table 4), in spite of a relatively heavy rate of cropping (86.2 pounds).

The similarity of standing crops in Beta in 1959, and in Beta and Gamma in 1960, and a consideration of "pounds gained" in the two periods (Table 4), suggested that from 170 to 180 pounds per acre was near the maximum carrying capacity of these ponds for smallmouth. This seems evident because final standing crops were similar in the three instances, and "pounds gained" was either high (133.8 pounds in Beta, 1959), or low (40.5 pounds in Gamma, 1960), depending upon the poundage required to attain this presumed maximum.

Large standing crops in Beta in 1959, and Beta and Gamma in 1960, suggested that these populations made highly efficient use of available foods, and it is of interest to examine their compositions. Table 6 presents numbers of each age class censused, with percentages of total weights and numbers of the entire population comprised by each.

A characteristic common to all three populations was the dominance of bass in the intermediate size ranges. In October, 1959, Age I fish in pond Beta ranged from 6.0 to 8.9 inches total length, and comprised 85.3 percent of the total populations by weight and 82.2 percent by numbers. In 1960, the principal component in both Beta and Gamma was Age II fish ranging from 7.5 to 10.9 inches in total length. By weight, these comprised 85.9 percent and 94.6 percent of the populations in Beta and Gamma, respectively. Predation of young may have made a major contribution to growth of the older fishes. In studies of the stomach contents of 59 Age I fish collected from these ponds, however, fish were a minor item, and various invertebrates strongly predominated. It seems obvious that the larger fish (6–11 inches) competed quite intensively with the smaller ones for invertebrate foods, and made efficient use of these foods when small fish were scarce or absent. This contrasts with the situation in pond Delta in 1959 where low production was attributed largely to an absence of small fish. In that instance, however, fish older than Age I were also limited, numbering only 32. An inference from the two populations may be that when a sufficient number of smallmouths are present to make efficient use of an abundant supply of invertebrate foods, size of the bass may be relatively unimportant, and the absence of young, small fish may cause little or no loss in total production of pounds of fish flesh.

Unfortunately, we had no population of large numbers of young fish only so that their efficiency could be compared with that of larger individuals of Ages I and II. However, we believe smallmouth of such intermediate sizes to be either superior foragers or more efficient converters of invertebrate foods than largemouth of a similar size, which, in our experience, exhibit more specific food requirements in the form of fish and other large food items.

Populations censused in 1959 had expanded through two seasons from an initial stock of 5.6 pounds, and ponds drained in 1960 had developed through one growing season from original stocks of 90, 91 and 97 pounds in Beta, Gamma and Delta respectively (Table 4). The data indicate that a sufficient amount of time had elapsed in both periods for carrying capacities to have been achieved. This conclusion is based on a comparison of "pounds gained" against standing crop totals. The data for pond Gamma provide one of several examples. When cropped in 1958 and 1959, the population in pond Gamma had a "pounds gained" figure of 137.2 over the 2-year period, as compared to only 40.5 pounds when "overstocked" in 1960. "Pounds gained" would probably have exceeded 40 pounds in 1960 had the pond not attained its carrying capacity at that point.

These results indicate substantial differences in productivities of ponds Beta, Gamma, and Delta during the smallmouth bass experiments. Beta and Gamma both clearly exceeded Delta in pounds of fish produced in both years of census. A greater productivity by Beta than Gamma in 1959 was indicated by the fact that although Beta received an addition of 41.7 pounds of stock, while Gamma was heavily cropped, surplus productions in the two ponds were

Table 6. — Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of smallmouth bass in the single pond Alpha, in ponds Beta, Gamma, and Delta (Unit 1), and in ponds Sigma, Tau, and Upsilon (Unit 4), in years indicated.

Pond, Year of Census, Treatment[a]	*Total Number Censused in each Age Group*					*Percent of Total Number Censused in Each Age Group*					*Percent of Total Weight Censused in Each Age Group*					*Total, All Age Groups*	
	0	I	II	III	IV & Older	0	I	II	III	IV & Older	0	I	II	III	IV & Older	Number	Pounds
A 1957 0	1,157	0	76	0	1	93.8	0.0	6.2	0.0	Tr	50.5	0.0	46.1	0.0	3.4	1,234	64.7
D 1959 0	0	2	26	6	0	0.0	5.9	76.5	17.6	0.0	0.0	3.1	69.6	27.3	0.0	34	26.4
G 1959 —	1	357	0	0	0	0.1	99.9	0.0	0.0	0.0	1.0	99.9	0.0	0.0	0.0	358	73.1
B 1959 +	188	1,009	20	8	0	15.3	82.2	1.6	0.4	0.0	3.8	85.3	5.4	5.5	0.0	1,225	180.0
B 1960 0	889	0	406	4	3	68.3	0.0	31.2	0.3	0.2	9.7	0.0	85.9	1.6	2.8	1,302	169.0
D 1960 —	67	0	126	2	2	34.0	0.0	64.0	1.0	1.0	5.9	0.0	85.9	2.7	5.5	196	56.3
G 1960 +	23	0	506	14	0	4.2	0.0	93.2	2.6	0.0	0.3	0.0	94.6	5.1	0.0	543	173.4
S 1961 0	70	0	0	233	8	22.5	0.0	0.0	74.9	2.6	1.4	0.0	0.0	91.2	7.4	311	84.9
S 1963 0	729	24	47	8	59	84.1	2.8	5.4	0.9	6.8	11.9	4.3	23.6	4.8	55.4	867	93.2
T 1963 —	77	11	0	0	1	86.5	12.4	0.0	0.0	1.1	31.6	51.1	0.0	0.0	17.3	89	9.3
U 1963 +	1,534	59	44	6	86	88.7	3.4	2.5	0.4	5.0	14.4	10.0	16.5	3.2	55.9	1,729	95.5

[a] Ponds are designated as: A = Alpha, B = Beta, G = Gamma, D = Delta, S = Sigma, T = Tau, and U = Upsilon. Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.

similar (133.8 and 137.2 pounds). That the productivity of Beta was as great as, if not greater than, that of pond Gamma in 1960 was evidenced by the fact that final standing crops were similar even though Gamma received 50.2 pounds of additional stock while Beta, the control, received none.

Standing crops measured by fall draining censuses of ponds in Unit 4 (Sigma, Tau, and Upsilson) ranged from 9.3 pounds per acre in the grossly overcropped Tau, to fairly uniform levels of from 84.9 to 95.5 in the two companion ponds. The two fall standing crops in pond Sigma, and the final one in pond Upsilon were thought to either exceed or to approximate carrying capacities of those ponds in the fall season, and such levels were about one-half of those measured in the fall in the more fertile ponds (Beta and Gamma) of Unit 1. In Unit 4 ponds, however, censuses were also made in the spring by Petersen estimates, and these data indicated fall carrying capacities greatly exceeding those of the spring. This is illustrated by data in Table 5, and in the following review of the known history of each population in Unit 4.

As shown in Table 5, standing crops recorded for control pond Sigma were 84.9 pounds by a draining census in the fall of 1961, 56.4 pounds by a Petersen estimate in the spring of 1963, and 93.2 pounds by the final draining census in October, 1963. Related facts of importance were, briefly, as follows. As shown in Table 6, the 1961 standing crop of 84.9 pounds was comprised primarily (91.2 percent by weight) of 233 individuals of the dominant Age III class. From the original stock of 343 Age III fish, 105 had been removed in 1961, leaving an unaccounted for loss, or mortality, of five individuals by the end of that first year. From the time of stocking in October, 1960, to October, 1961, the 233 survivors of the original stock of 343 had made an average length increment of only 0.24 inches, had shown an average loss in weight of 0.012 pounds, and a loss in condition of from 4.5 to 4. None of the original 311 fingerlings stocked at Age O were recovered in 1961, apparently having been lost through predation, and the recovery of only 70 Age O fish in the 1961 census represented the total recruitment to the population. There was a deficit by October, 1961 of 9.8 pounds, as shown in the "pounds lost or gained" column of Table 5, in spite of the earlier cropping of 36.1 pounds. The combination of these facts indicated that the final standing crop of 84.9 pounds may have exceeded the carrying capacity of the pond at the time of the 1961 census. For this reason, all three populations in this unit were again thinned in May and June, 1962. The removal from pond Sigma was 143 8- to 10-inch bass (then Age IV), weighing a total of 50.5 pounds. Concurrent removals from the companion ponds were similar, and will be given in the discussions concerning each.

Pond Sigma was next inventoried by the Petersen method in the spring of 1963, and this inventory provided an estimated standing crop of 56.4 pounds. Recoveries made in the fall draining census indicated this estimate to be accurate. Using the figure of 56.4 pounds, we computed a pounds gained of only approximately 15 pounds since the previous inventory in October, 1961, in spite of the removal of 50.5 pounds of bass at the start of the 1962 growing season. It is therefore believed that the carrying capacity of pond Sigma in the spring of 1963 was quite low, and probably almost the same as the standing crop of 56.4 pounds estimated at that time.

The 1963 draining census of pond Sigma yielded a standing crop of 93.2 pounds. Based on an "original stock" of 56.4 pounds as provided by the 1963 spring estimate, we derived a pounds gained figure of 37.4 during the 1963 growing season. This rather substantial gain (as compared with those of 1961 and 1962) was coupled with an increase in condition by the dominant age group of from 4 in October, 1961, to 5 in October, 1963. We therefore believe that the carrying capacity of pond Sigma was substantially higher in the fall of 1963 than at either previous census, and that the increase was due primarily to an increasing fertility and a consequent greater food production, with the food increase being primarily in the production of scuds and crayfish.

Increased production in pond Sigma may also have been related to changes in population composition. The 1961 draining census contained only 70 fish of Age O, none of either Ages I or II, and 241 that were Age III or older. The 1963 census contained 729 Age O fish, 24 of Age I, 47 of Age II, and 67 that were Age III or older. With its more normal distribution of sizes, the 1963 population would be expected to have made a more efficient use of available foods.

The cropped pond, Tau, was inventoried by a Petersen estimate in the spring of 1963, and by a draining census in October, 1963. We believe that the standing crop of about 5.6 pounds estimated in April, 1963, was quite accurate (Table 5). At the final draining census (October, 1963) the population contained only 89 fish weighing about 9.3 pounds, of which only 12 were older than Age O and only one older than Age I. Clearly, the cropping of a total of 119.4 pounds from this pond in 1961 and 1962 was excessive. Remaining fish grew fast, and were in excellent condition, but there were too few to efficiently exploit the increasing availability of food. Expansion of the population was further inhibited by a failure of reproduction in 1963, although reproduction was successful in both companion ponds. Though cropping had been heavy, our accounting indicated that a minimum of 30 adults should have been available for spawning in 1963. Mortalities apparently exceeded the expected, and may have left no breeding pairs. An additional cause for failure may have been the great abundance of crayfish in this pond at the time of spawning. In a later study, in a 4-acre pond containing smallmouth, lake chubsuckers, *Erimyzon succeta* (lacépède), and chain pickerel, we credited the foraging of an extreme abundance of crayfish with destroying the eggs and/or larvae of lake chubsuckers and chain pickerel.

By midsummer 1963, it was clear that no Age O fish were present in pond Tau, and on July 26, 97 Age O fingerlings were transferred to Tau from Upsilon. When censused in October, 77 of the 97 (79.4 percent survival) were recovered. Based on an original stock of 5.6 pounds, as estimated in April, 1963, and 7.5 pounds removed, this cropped pond made a gain of only about 10.8 pounds during 1963. The fish grew well in the presence of abundant food, but were simply too few in number to make additional gain.

Standing crops recorded for the addstock pond Upsilon were 55.4 and 64.5 pounds from Petersen estimates in the springs of 1962 and 1963, respectively, and a total of 95.5 pounds from the draining census of October, 1963. The dynamics of this population are also quite thoroughly known, and will be reviewed in some detail.

Intensive sampling indicated that all 313 Age O fingerlings stocked in October, 1960, and all but few of a large 1961 brood were eliminated by fall of 1961, probably by predation.

From the original stock of 346 fish of the 1958 year-class, we had removed a total of 102 (early thinning, stomach samples, etc.), and during a scheduled transfer operation in the summer of 1961 we had added a total of 120, leaving a balance of 364 1958 year-class fish at the beginning of the winter of 1961–1962 (assuming no 1961 mortality). The Petersen estimate of May, 1962, indicated that the total population consisted of 180 individuals. Based on average weights at that time the standing crop was computed to be 55.4 pounds, or about 43 percent of the total weight (129.6 pounds) originally stocked. This indicated a mortality of 184 bass of the 1958 year-class, weighing approximately 67 pounds. Since average condition of this year-class had declined during the previous season (1961) from 4.5 in April, to 3.6 in September, the mortalities were not unexpected. We decided, however, that the population should be further reduced. On May 10, 1962, 55 additional bass of this age were removed. Based on our previous estimate of 180 fish, this left a total of 125 of the 1958 brood to enter the 1962 growing season. A subsequent increase in condition from 3.7 in May, to 5 in July, indicated the thinning had significant results.

Over the course of the 1962 season 3 bass of the 1958 year-class were injured and removed, and 37 were added as a part of the regular transfer program. Assuming no additional mortalities, we should have ended the 1962 season with 159 individuals of the year-class in question.

The population in pond Upsilon was again inventoried by a Petersen estimate in May, 1963. The estimate indicated an overwinter mortality of about 78 fish, or about half the number that died during the previous winter. Such an estimate would have put us into the 1963 season with 81 fish of the still dominant 1958 brood. Finally, using the October, 1963 census figures, we can evaluate our previous estimates of standing crop and mortalities for this group. We entered the spring with an estimated 81 Age IV fish, and one fish of this age was transferred into Upsilon in July. The final census yielded 83 fish of this age, indicating that our earlier estimates of this dominant 1958 year-class had been surprisingly good.

The final standing crop (drain census) in pond Upsilon in October, 1963 was 95.5 pounds. Based on the 1963 spring estimate of 64.5 pounds, we derived a pounds gained figure for 1963 of 26.2 pounds. The carrying capacity of Upsilon apparently improved during this third season over what it had been at previous times of census, and to the level of that attained by pond Sigma at the end of its third year. Again, increased production was probably due to increased fertility, greater food production (principally crayfish and scuds), and a more efficient distribution of sizes within the 1963 population. Whereas the October, 1961 population was dominated by excessive numbers of adults of the 1958 year-class that were in extremely poor condition, the 1963 population contained a more normal and efficient distribution of sizes (Table 6).

As shown in Table 3, maximum standing crops attained in Sigma and Upsilon (Unit 4) were just about half of those attained in Beta in 1959 (180 pounds), and Beta and Gamma in 1960 (169 and 173.4 pounds). This difference in productivity was much larger than anticipated, and had caused us to grossly overstock the Unit 4 ponds at the time of transfer.

Effects of Cropping and Adding Stock

The effects of cropping and adding smallmouth stock on the production of fish flesh were largely obscured in these experiments by differences in the productivities of contiguous ponds in Unit 1, and by the effects of gross overstocking, and subsequent overcropping of the cropped pond, in Unit 4. The data to be considered are those listed under the column headed "pounds lost or gained" in Table 4. This figure of "pounds gained," closely analagous to the surplus production of Ricker (1958) and Cooper *et al.* (1963), should have been highest in cropped ponds, lowest in the ponds receiving added stock, and intermediate in the control ponds.

The highest individual gain was that of 137.2 pounds in cropped Gamma over the 1958–1959 period, but the average for cropped ponds was made abnormally low because of limited production in pond Delta in 1960, due to this pond's fertility being lower than in either companion pond, and by the low production in pond Tau caused by the severe overcropping of this population. The average for control ponds was also lower than should have occurred because of abnormally low production in pond Delta in 1959, due to the paucity of numbers available to add flesh, and in pond Sigma in 1961, because no gain was possible due to original, gross overstocking. On the other hand, the average gain in fish flesh probably was higher in the add-stock ponds than should have occurred because pond Beta was more fertile than either companion pond, and made the large gain of 133.8 pounds of fish flesh over the 1958–1959 period in spite of an addition of 41.7 pounds of stock. As mentioned previously, this higher production in Beta was probably related primarily to the manner in which this pond was supplied with water and the enrichment of its food supply by the entrance of drift organisms from the feeding stream.

Growth and Condition

Two types of growth data are presented. For comparison with smallmouth growths made in other waters, our data in Table 7 represent averages of all fish of the respective age classes recovered in the October censuses. Most ages were known by length ranges (particularly for the youngest age class present), or by the presence or absence of a particular fin clip. Fish of uncertain age were omitted from Table 7. Addi-

Table 7. — Growth of smallmouth bass in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on smallmouths in several other waters.[a]

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
......	Alpha	1957	None	4.0(1,157)	. .	. .	. .
Unit 1	Beta	1959	Add-stock	4.3(188)	7.1(1,009)	10.4(20)	. .
	Gamma	1959	Cropped	4.7(1)	7.6(357)	. .	. .
	Delta	1959	Control	. .	9.2(2)	11.3(26)	. .
Unit 1	Beta	1960	Control	3.4(899)	. .	9.3(406)	11.4(4)
	Gamma	1960	Add-stock	3.8(23)	. .	9.0(506)	11.6(14)
	Delta	1960	Cropped	4.7(67)	. .	9.4(126)	11.9(2)
Unit 4	Sigma	1961	Control	3.4(70)	. .	. .	9.4(233)
	Sigma	1963	Control	3.2(729)	7.0(24)	9.8(47)	. .
	Tau	1963	Cropped	4.1(77)	9.2(11)	. .	. .
	Upsilon	1963	Add-stock	2.7(1,534)	6.8(59)	9.0(44)	10.0(6)
Other Waters		*Author*					
Jordan Creek, Ill.[b]		Durham (1955)		3.3	6.3	9.5	11.4
Malcomson's Pond, Ill.[c]		Bennett & Childers (1957)		5.3	9.3	11.1	12.2
Siloam Springs Lake, Ill.[b]		Rock (1966)		4.2	7.0	10.5	13.2
Michigan[c]		Beckman (1949)		5.9	9.0	11.2	13.3
Norris Reservoir[b]		Stroud (1948)		3.1	8.9	13.3	15.8

[a] All data from our ponds are for fish of known age.
[b] Lengths back calculated from scales.
[c] Average lengths of fish separated on the basis of ages assigned from scale analysis.

tional growth data are presented in Fig. 2 and 3 where growth curves are based on samples collected during the months indicated.

Linear growth in our single-species populations was somewhat intermediate to growth made in other waters through the first 2 years of life, but in some cases was quite poor thereafter (Table 7). Extremely poor growth by the third, fourth, and fifth year fish was due to overcrowding (most notably in Unit 4), or to the scarcity of large food items such as small fish or crayfish.

Fig. 2 presents growth and condition curves for the dominant 1958 brood through the 1960 season in ponds Beta, Gamma, and Delta. Near cessation of growth in ponds Gamma and Delta from mid-May to mid-June was paralleled by a deflection in condition curves. Condition of the cropped population made a sharp improvement in June and remained high for the remainder of the season, and this was paralleled by rapid and continuous growth through September. Data from the control pond illustrates an inconsistency that was rather common throughout this study. Here a high rate of growth was paralleled by a declining rate of condition. During this same period both growth and condition in the add-stock population remained low.

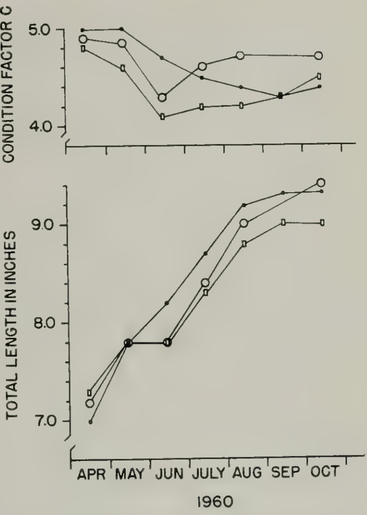

Fig. 2.—Growth and condition (C) of smallmouth bass of the dominant 1958 year-class in the control pond Beta (dots), add-stock pond Gamma (rectangles), and cropped pond Delta (circles) during the 1960 growing season.

The growth and condition curves showed only moderate conformity to the differing densities of stock. When stocked in October, 1959, each pond had received approximately 455 bass of this dominant age group (Age II in 1960). Cropping and transfers of stock during 1960 included 321 bass of Age II weighing 75.5 pounds, cropped from pond Delta, of which 175 weighing 41.4 pounds were marked and released in pond Gamma. Comparative densities at the time of the October, 1960 censuses were 406 in the control pond, 126 in the cropped pond, and 506 in the add-stock population (Table 6). With a final ratio of densities as great as 4:1 (506 to 126) between the add-stock and cropped populations, one would have expected a greater influence on growth and condition than seems to have occurred. Again, we suspect that the influence of the treatment was masked by differences in the ponds' productivities, with pond Delta again indicated to have a low productivity.

As mentioned earlier, growth by larger fish was extremely poor in the infertile, generally overcrowded ponds in Unit 4. This is emphasized in Table 8 which shows total length and weight increments of the dominant 1958 year-class over the period 1961–1963.

Growth and condition curves of the 1958 year-class through 1960 were plotted in Fig. 2, and following the transfer of the population to the new unit of ponds we may again trace this dominant age group through its 3-year

Table 8. — Length and weight increments over three seasons, 1961–1963, and final average coefficients of condition for the dominant 1958 year-class of smallmouth bass in ponds Sigma, Tau, and Upsilon.

Pond	*Treatment*	*Average Length Increment, Inches*	*Average Weight Increment, Pounds*	*Final Average Condition (C)*
Sigma	Control	2.68	0.80	4.9
Tau	Cropped	4.17	1.61	6.8
Upsilon	Add-stock	1.51	0.61	4.8

history in ponds Sigma, Tau, and Upsilon (Fig. 3). Again growth and condition were computed from the same samples. While mid-season samples were in some cases quite small, and a source of some error, those collected at the beginning and end of each season were large and believed to be highly representative. Because of initial overstocking of all three ponds with approximately 130 pounds per acre, growth was negligible, conditions remained poor, and the influence of the experimental treatment was only barely discernible in 1961. All three populations were heavily and equally thinned in early 1962, and the effects of subsequent cropping and transfer of stocks became increasingly apparent throughout 1962 and 1963.

The degree of conformity between the growth and condition curves indicates that for the 1958 year-class in Unit 4 ponds there was a rather close relationship between rate of growth and body condition, with fastest growth associated with best condition, and vice versa. The most dramatic response to population manipulation occurred among the dominant 1958 year-class in pond Upsilon. Average condition for these fish declined from 4.5 in April, 1961, to 3.6 in the following September, due to increased density of stock.

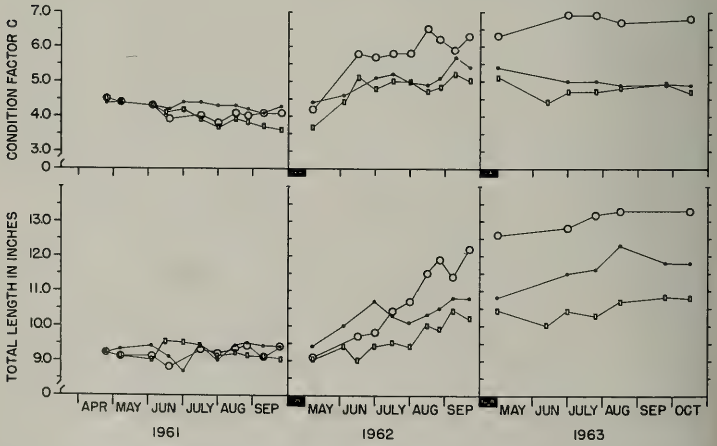

Fig. 3.—Growth and condition (C) of smallmouth bass of the dominant 1958 year-class through three growing seasons (1961-1963) in the control pond Sigma (dots), cropped pond Tau (circles), and add-stock pond Upsilon (rectangles).

A combination of overwinter mortality, and additional thinning by us in May, 1962, caused condition of this population to improve from 3.7 in May, 1962, to 5 by the following June.

Mortalities

Mortality data for the populations of smallmouth in ponds Beta, Gamma, and Delta were for three categories of fishes: 1) those of the original stock, 2) those transferred from the cropped to the add-stock pond, and 3) those fish captured, measured, weighed, marked, and released when and where caught. Mortalities over the 1958–1959 period for bass of the three year-classes transferred from Gamma to Beta in 1959 ranged from 50 percent for the 1956 year class, to 100 percent for the 1958 year class, averaging about 70 percent; whereas mortalities over a single season for those marked and transferred from Gamma to Beta in 1959 ranged from 38.1 to 75 percent, averaging about 51 percent. Among 294 fish of the 1958 brood transferred from Gamma to Beta during 1959, the mortality by the end of that season was 38.1 percent, while for 144 fish of the same age caught in Beta, marked, and returned to Beta, the comparable mortality was 34 percent. For older fish of the 1957 brood, comparable figures were 40 and 36.7 percent, in almost the same ratio. In this instance the transferred fish survived quite well in the new population, and the act of transfer was in itself no cause for a notable increase in mortality. In 1960, however, we found the mortality among 175 fish transferred to pond Gamma was 25.1 percent, as compared to 17 percent among the 168 fish which were caught in Gamma, marked, and returned to the same population in that pond. As in the 1959 data, mortalities of the younger and older fish in 1960 generally were higher than those of intermediate ages. Finally, average rates of mortality were greater in the add-stock pond, intermediate in the control pond, and lowest in the cropped pond.

Mortalities as related to densities of stock are best known for the 1958 year-class of bass during their third year of life in the 1960 season. When restocked in October, 1959, each pond received from 449 to 455 fish of this age class. Recoveries, numbers unaccounted for in the census, and percents of mortalities by October, 1960, for various categories of these bass are shown in Table 9. Following the removal of 321 individuals from the cropped population, only 8 fish were unaccounted for in the October census, indicating a mortality of 6 percent among that portion of the original population that was not cropped. Comparable figures were 7.9 percent in the control population, and 13.2 percent among the original stock in the add-stock population. Among those fish

Table 9.—Numbers of the dominant 1958 year-class of smallmouth bass originally stocked in ponds Beta, Gamma, and Delta in 1959, numbers cropped and added in 1960, and numbers of the different categories recovered in the draining censuses, with numbers of fish unaccounted for, and percents of mortality.

Pond	*Number Originally Stocked, Oct., 1959*	*Number Cropped from Pond in 1960*	*Number Transferred to Pond in 1960*	*Number of Original Stock Recovered in Census, Oct., 1960*	*Number of Transferred Fish Recovered in Census, Oct., 1960*	*Number Unaccounted for*		*Percent Mortality*	
						Original Stock	Transferred Fish	Original Stock	Transferred Fish
Beta	449	8	0	406	..	35	..	7.9	..
Gamma	452	20	175	375	131	57	44	13.2	25.1
Delta	455	321	0	126	..	8	..	6.0	..

transferred to the add-stock population, mortalities were 25.1 percent, approximately twice as great as among survivors of original stock in this same pond. It should be pointed out here that neither the marks used, nor the handling of fish involved in the transfer of stock, were in themselves causes for increased mortalities. The transfers were accomplished in conjunction with our regular sampling operations, and frequently more fish were caught, marked, and returned to the control pond than were marked and transferred from the cropped to the add-stock population. The transferred fish were simply carried a few feet farther, in water, before their release. Thus, where mortalities were greater among fish that were marked and transferred than among resident individuals that were marked and returned to the same pond, those mortalities must be attributed to something other than the purely physical effects of the marking and transfer. In this instance it was probably an inability to compete on even terms with those fish already resident in the overcrowded population.

The inability of transferred fish to compete effectively with those resident in an overcrowded population also was evident in a study made of rates of seasonal mortalities of smallmouth bass in 1960. Rates of mortalities were based on recoveries in the draining censuses of fish given distinctive fin clips for each month of the 1960 growing season (Table 10). Marked fish were principally of the 1958 brood. Errors due to incomplete recoveries are believed to have been small, and such errors would operate in favor of lower mortalities. Mortalities due to marking were erratic, and high for some marking periods, as is clear from a study of Table 10. For example, the returns of fish marked in April implied that percentages of from 26.7 (in Beta) to 30 (in Gamma) of all fish of the group in question that were living at the time of marking had died by October. Actually, total rates

Table 10.—Numbers of adult smallmouth bass marked each month in the April-September period of 1960 in categories indicated, numbers recovered in the draining censuses of October, 1960, and percents of mortality for each group. Of the total of 548 fish marked, all but 32 were assigned to the 1958 year-class.

Month	*Marked and Returned Directly to the Control Population, Beta*			*Marked and Returned Directly to the Add-stock Population, Gamma*			*Marked and Transferred to the Add-stock Population, Gamma*		
	Number Released	Number in Census	Percent Mortality	Number Released	Number in Census	Percent Mortality	Number Released	Number in Census	Percent Mortality
April	30	22	26.7	29	21	27.6	30	21	30.0
May	30	28	6.7	30	24	20.0	31	22	29.0
June	30	29	3.3	30	26	13.3	48	30	37.5
July	31	31	0.0	31	23	25.8	57	48	15.8
Aug.	30	30	0.0	29	27	6.9	22	16	27.3
Sept.	30	24	20.0	30	24	20.0	. .	. .	. .
Total	*181*	*164*		*179*	*145*		*188*	*137*	
Average			*9.4*			*18.9*			*27.9*

of mortality for the year-class in question (1958) over the entire 12-month period were only 9.6 percent in Beta, and 17 percent in Gamma. Marks used were clearly distinguishable at the time of the draining censuses, and there seemed to be small margin for error in their interpretation. These data indicated that such studies must be conducted with great care, and should involve large samples. In the present instance the "unnatural" death of as few as four or five fish projected serious errors.

Mortalities were not proportional to length of time marked, due possibly to greater deaths among marked fish in certain months than others. However, if such errors (deaths) may be assumed to have been reasonably proportional for each population, a significant and logical pattern appears when rates of mortality for fish marked each month are averaged for each category over the season (see averages in Table 10). Average rate of mortality was lowest in Beta, the control pond, intermediate for those marked and returned in the "add-stock" pond, and highest for those transferred from Delta to the add-stock pond.

Our principal data on mortalities in the ponds in Unit 4 are from fish of the dominant 1958 brood in the control and add-stock populations. As observed for our earlier smallmouth populations (Table 10), mortalities were lowest in the control pond and highest in the add-stock pond, and seemingly related to density of stock. For example, in the control pond Sigma, with an original stock of 343 Age III fish on October, 1960, the year-class had an unaccounted for loss of only 5 individuals by October, 1961, and an additional loss of only 29 individuals by October, 1963. In this instance, 105 fish had been removed in 1961 and five were unaccounted for, leaving 233 survivors in the 1961 fall census. Assuming removals and deaths had been nonselective as to size, over the 12-month period the 233 survivors had made an average length increment of only 0.24 inches, and had shown an average loss in weight of 0.012 pounds and a loss in condition of from 4.5 to 4. Living conditions were therefore quite poor, but not so poor as to have induced mortality.

Such low rates of mortality in pond Sigma in 1961 were verified by the following experiment. For each month from April through September, from 28 to 30 individuals of the 1958 brood were caught and released with a mark distinctive for that month. When censused following pond draining in October, 1961, recoveries were made of 28 of the 30 fish marked in April, 28 of the 30 marked in May, and of 100 percent of fish marked in each of the four remaining months. Of the two fish missing from each of the April and May samples, one for each month, or two of the total of four, were observed, accidental deaths. There were therefore only two unaccounted for individuals among the 176 fish marked, and mortalities for this group were less than 2 percent.

In the add-stock pond Upsilon, with its steadily increasing density of stock, mortalities became quite high. Assuming no mortalities, we would have entered the winter of 1961–1962 with 325 individuals of the 1958 year-class. Our 1962 spring estimate indicated a population of only 180, and a mortality to that date of 184 individuals. Average condition had declined through 1961 from 4.5 in April to 3.6 in September, so large overwinter mortality was not unexpected. Our next inventory by Petersen estimate in April, 1963, indicated that an additional 78 fish of this group were missing and unaccounted for. While both estimates could have been in error, the sum of estimated mortalities from both was verified by the 1963 final census. The two estimates had indicated 81 survivors by April-May, 1963, and a transfer from Tau raised the total to 82. Thus, a recovery of 83 individuals in the final census indicated that the estimates had been exceptionally good.

While mortalities were high in the add-stock pond, this population was subjected to considerable stress by virtue of the greater population density and a limited food supply. There may have been an additional stress owing purely to the transfer and adjustment to a new environment. Quite possibly the impact of the transferred fish may have created stress for the resident fish as well. On the other hand, mortalities in the control pond were extremely light. Results from the control pond indicated the adult smallmouth bass to be unusually hardy, even under the relatively poor conditions afforded by pond Sigma, and even when subjected to frequent sampling by seine, shocker, or hook-and-line, and to multiple marking by fin clip. In this respect, we experienced the smallmouth bass to be a much tougher and superior experimental fish than the largemouth.

Spawning Success

In 1960 an effort was made to study success of spawning and survival of young in relation to the differing densities of populations in the three ponds in Unit 1. Table 11 presents 1) estimates made of the number of potential spawners in each pond, 2) counts made of total numbers of nests and numbers of successful nests, 3) percentages of successful nests, 4) ratios of numbers of total nests and of successful nests to numbers of spawning adults, and 5) estimated numbers of fry produced and their rate of mortality by the time of the October draining censuses.

The potential number of spawning adults was taken as the number of fish of Age II (1958 brood) or older stocked in each pond the previous November, plus or minus those added to or removed from each pond prior to the advent of

Table 11.—Estimated numbers of potential smallmouth bass spawners, counts of nests and of successful nests, percents of successful nests, ratios of nests to potential spawners, and ratios of successful nests to potential spawners in ponds Beta, Gamma, and Delta, 1960.

Pond	*Estimated Number of Potential Spawners*	*Count of Nests*	*Count of Successful Nests*	*Percent of Successful Nests*	*Ratio of Nests to Potential Spawners*	*Ratio of Successful Nests to Potential Spawners*	*Estimated Number of Young Produced*	*Number of Young Recovered in Census*	*Percent Mortality of Young*
Beta	463	122	40	32.8	1:3.8	1:11.6	21,930	899	95.9
Gamma	526	157	6	3.8	1:3.4	1:87.7	3,290	23	99.3
Delta	344	133	20	15.0	1:3.5	1:23.2	10,965	67	99.4

spawning in late May, 1960. The assumption of no overwinter mortality is undoubtedly erroneous; however, deaths through the winter were known not to have been large. Counts of nests, and of successful hatches of fry were made by dividing each pond into small sections and making daily counts of all sections throughout the spawning period. Estimated production of fry was computed from an average number of fry per nest based on actual counts of fry taken from the nests. The black but still largely immobile sac-fry were siphoned out of the nests and spread over the bottom of a large white enameled tray having a grid marked in the bottom. Pictures were taken and later enlarged so that counts could be made in the laboratory. The fry were sucked off the nest by means of a ¾-inch tube attached to the bottom of a 5-gallon bucket. Slow submersion of the bucket from above created a gentle suction by which the fry could be moved from the nest into the bucket. When fry were returned to the nests the guarding males resumed their patrols, and all such spawns were observed to develop in a normal fashion. Successful counts were made of broods removed from eight nests, six from pond Beta, two from pond Delta. The overall range in numbers of fry per brood was from 190 to 787. The six broods from pond Beta averaged 542 fry per brood; the two from pond Delta averaged 568. The average of the eight nests was 548.25, and this figure was used as the basis for computing the total productions of fry listed in Table 11.

It may be significant that pond Gamma with both the largest number of potential spawners and the largest number of nests, had by far the lowest rate of spawning success (Table 11). This would appear to be a density-related factor whereby overcrowding brought about a reduced reproduction. Ricker (1954) presented reproduction curves exhibiting this phenomenon in a variety of animal populations, and Rose (1959) presented evidence of reduced reproduction as a result of overcrowding guppies. However, the relation of spawning success to density of the spawning population was not consistent in data from ponds Beta and Delta. Pond Beta had an intermediate number of spawners and the smallest number of nests, but had the greatest number of successful nests, whereas Delta with the smallest number of potential spawners had an intermediate number of nests and an intermediate number of successful nests. Though density related, rate of spawning success in the present data appeared related to additional factors as well. One such factor may have been the relative locations of the ponds, and the manner in which they received water. As mentioned earlier, the supply stream first entered Beta, from which it overflowed to fill Gamma, from which it again overflowed to fill Delta. It may be significant that pond Beta, the first pond in the series, is believed to have had the most successful rate of reproduction and/or survival in all 3 years, 1958–1960. Reproduction in Delta, the last in the series, was extremely limited in 1958, and believed to be nonexistent in 1959, and in both years was less than that achieved in pond Gamma, the middle pond in the series. Thus, in both 1958 and 1959 the rate of spawning success decreased in the exact order in which the ponds were located in the flow series, from Beta to Gamma to Delta. The order was partially reversed in 1960, with a greater production of fry in Delta than in Gamma. In this instance, however, the much greater density of breeding stock in Gamma than in Delta (Table 11) may have had an overriding influence.

The significance of the position of the ponds in the flow series could be related to an accumulation of an inhibitory product. Rose (op.cit.) demonstrated in aquaria that some fishes release waterborne products that limit growth and survival of their own or closely related species, though not limiting that of certain other distantly related forms. Rose's studies also suggested that self-inhibiting products produced by one species may be metabolized away by other species in the community. Thus, a species maintained alone might be more subject to such an inhibitory influence than when in a mixed population. Although the ponds contained no fish when filled, they received additions of "make-up" water throughout the course of the experiments. Thus, an accumulation of waterborne products would have been progressively greater in Gamma and Delta, and if such an inhibitory influence was operative it would have decreased production and survival of young in the order in which it occurred.

Total counts of nests and of successful nests were not possible in the Unit 4 ponds because of higher water turbidities. However, in the 1961 spawning season a reliable count was believed made of broods of fry just risen from the nests. Each such brood was marked with a float at the point first seen, which in most cases was very near to a nest. The totals of floats in each pond is believed to have closely approximated the totals of broods. Table 12 presents the number of broods seen, the time intervals over which they were seen, the number of potential breeders believed to have been present, and computed ratios of numbers of broods to number of potential spawners. As earlier observed in Unit 1 (Table 11), the fewest number of hatches was associated with the greatest density of breeding stock. Pond Upsilon with an estimated 348 breeders (1958 year-class and older), produced only 7 hatches, for a ratio of about 1:50. Comparable ratios were 1:14 in Sigma, with an estimated 292 breeders, and about 1:17 in pond Tau with approximately 237 potential spawners.

Brood counts were also made in 1962 and 1963, but poorer visibilities, due principally to frequent strong winds, probably made these counts less complete than those of 1961, and they were not included in the table. In 1962 our notes listed only five hatches observed in the add-stock pond, as compared to nine in the control, Sigma, and either "eight or nine" in the cropped pond Tau. No hatches were observed in pond Tau in 1963, due, possibly, to the absence of a breeding pair because of overcropping, or to predation of eggs or larvae by an abnormally large population of crayfish.

Foods of Smallmouth Bass

Information on foods eaten in ponds Beta, Gamma, and Delta is based on examination of 20 stomachs each from ponds Beta and Gamma and 18 from pond Delta, all of Age II, collected in June and August, 1960 (Table 13). Based on frequency of occurrence in stomachs, scuds and mayfly nymphs ranked first and second, respectively, in both June and August. Cladocerans and crawling water beetle larvae were also prominent in June, but much less so in August. Nymphs of damselflies were

Table 12. — Estimated numbers of potential smallmouth bass spawners, numbers of broods seen, time intervals over which they were seen, and ratios of numbers of broods to numbers of potential spawners in ponds Sigma, Tau, and Upsilon, 1961.

Pond	*Number of Potential Spawners*	*Number of Broods*	*When Broods Were Seen*	*Ratio of Broods to Potential Spawners*
Sigma	292	21	June 1–16	1:14
Tau	237	14	June 6–9	1:17
Upsilon	348	7	June 6–16	1:50

Table 13. — Food organisms found in stomachs of the dominant 1958 year-class of smallmouth bass collected from ponds Beta (control), Gamma (add-stock), and Delta (cropped) in June and August, 1960. Length ranges of the fish, in inches, were 7.8–9.8 in Beta, 7.4–9.3 in Gamma, and 7.2–9.7 in Delta.

Food Organisms		*Total Number of Items, All Stomachs*			*Percent of Occurrence, All Stomachs*		
		Beta[a]	Gamma[b]	Delta[c]	Beta[a]	Gamma[b]	Delta[c]
AQUATIC INSECTS							
Plecoptera	adults	0	1	0	0.0	5.0	0.0
Ephemeroptera	nymphs	60	210	691	50.0	70.0	69.0
Odonata							
Zygoptera	nymphs	40	6	101	60.0	25.0	25.0
	adults	22	1	2	25.0	5.0	11.5
Anisoptera	nymphs	5	0	0	20.0	0.0	0.0
Hemiptera							
Corixidae	adults	1	2	1	5.0	10.0	5.0
Coleoptera							
Haliplidae	larvae	0	395	440	0.0	40.0	25.0
	adults	3	0	2	10.0	0.0	12.5
Dytiscidae	larvae	3	0	16	15.0	0.0	30.0
	adults	0	1	5	0.0	5.0	19.0
Hydrophilidae	adults	0	0	1	0.0	0.0	6.5
Trichoptera	larvae	8	1	1	25.0	5.0	5.0
Diptera							
Culicidae	larvae	0	2	1	0.0	10.0	6.5
Tendipedidae	larvae	1	104	36	5.0	35.0	34.0
	pupae	0	13	67	0.0	25.0	37.5
Ceratopogonidae	larvae	1	5	0	5.0	15.0	0.0
	pupae	0	1	0	0.0	5.0	0.0
OTHER AQUATIC ORGANISMS							
Annelida							
Hirudinea		0	1	0	0.0	5.0	0.0
Cladocera		452	242	1,099	15.0	50.0	20.0
Ostracoda		3	12	0	10.0	30.0	0.0
Amphipoda		716	598	962	55.0	85.0	75.0
Decapoda		2	0	1	10.0	0.0	6.5
Hydracarina		2	62	65	10.0	25.0	52.5
Pisces		1	0	1	5.0	0.0	5.0

[a] Twenty stomachs examined, 18 of which contained food.
[b] Twenty stomachs examined, 19 of which contained food.
[c] Eighteen stomachs examined, all of which contained food.

moderately prominent in both periods. The prevalence of cladocerans in the stomachs of these smallmouth bass in their third year of life emphasized their dependence upon invertebrate foods. Fish remains were found in one stomach in June, crayfish in three stomachs in August. Smaller fish of Ages O and I undoubtedly utilized the same invertebrate foods. Larger fish of Age III and older appeared to prey to a considerable degree on fishes in Age I, and made fair growth so long as they were present, and grew poorly when they were absent. For example, in 1959 Age I fish were available in all ponds and fish older than Age II increased in length from an average of 12.5 inches in May, to 14 inches in October. In 1960, when Age I fish were not available, seasonal growth of the older and larger fish was negligible. Absence of a prey fish of a suitable size caused the elimination of many of the larger predators in an indirect way. In the last weeks of the 1960 season several of the larger fish were found dead with an Age II fish lodged in the gullet. Their hunger was obviously such that they were forced to prey on fish larger than their gullets could accommodate.

In 1960 an attempt was made to measure the standing crops of invertebrates in ponds Beta, Gamma, and Delta by collecting them in a large filter box of saran screen as described by Buck & Whitacre (1960). As the ponds were drained the water was screened through the box and the organisms collected and weighed. The only separation possible was that between "plankton" and scuds. The "plankton" consisted in the main of cladocerans, a moderate number of phantom larvae, and occasional copepods, water mites, small beetles, various nonburrowing mayfly nymphs, and scuds. This group was collected at a fairly continuous rate throughout the draining, except that the scuds drained out at the end of the operation, or concentrated in and around the sump at the end of the drain tube inside the pond. The technique worked reasonably well except for the fact that an unknown percentage of such forms as scuds, and the immature stages of caddis flies and mayflies, remained in the abundant dewatered vegetation in Beta and Gamma, while a greater percentage flushed out of the much less densely vegetated Delta. Recoveries of scuds and other larger forms could not be considered complete or comparable for all ponds, but that of "plankton" may have been reasonably so.

Weights obtained were as follows:

Beta	"Plankton"	37 lbs.
	Scuds	20 lbs.
Gamma	"Plankton"	142 lbs.
	Scuds	20 lbs.
Delta	"Plankton"	670 lbs.
	Scuds	131 lbs.

Differences in standing crops suggest a greater productivity for pond Delta, a fact not substantiated by the fish data. The vegetation factor, as mentioned above, would have accounted for a part of the differential, and may have accounted for it all. It should also be pointed out that standing crops of smallmouth were at least three times as great in both ponds Beta and Gamma as in Delta. Heavier rates of cropping of the "plankton" and scuds by the larger populations of fish could have caused the difference in standing crops of the invertebrates. With heavier rates of cropping, rates of production of invertebrates actually may have been greatest in the ponds having the smallest standing crops of invertebrates.

Information on foods eaten by smallmouth in Unit 4 ponds is based on a collection of 119 stomachs, 40 each from ponds Tau and Upsilon and 39 from pond Sigma. About 10 specimens were collected from each pond in each of the four months June through September. All samples were collected by hook-and-line, and the monthly samples from each of the three ponds were collected on approximately the same dates — June 16-20, July 24-25, August 22, and September 19. All specimens were adults of the dominant 1958 brood and ranged in length from 7.7 to 10.2 inches total length in June and from 8 to 10.8 inches in September.

A total of 105, or approximately 88 percent, of the 119 stomachs contained food; 14 were empty. Determinations were made of the number of items of each identifiable taxonomic group, their total volume in each stomach, their frequency of occurrence, and the average volume of food in stomachs containing food. A total of 23 items were identified in the stomachs (Table 14), but many were occasional or rare, and only six items were encountered with sufficient frequency, or in sufficient volume, as to be considered prominent. On the basis of frequency of occurrence the six most common items were 1) midge larvae and pupae in 46 stomachs, 2) burrowing mayfly nymphs in 42, 3) nymphs of smaller, nonburrowing mayflies in 39, 4) caddis fly cases in 24, 5) damselfly nymphs in 18, and 6) crayfish in 14. By

Table 14. — Food organisms found in stomachs of the dominant 1958 year-class of smallmouth bass collected from ponds Sigma (control), Tau (cropped), and Upsilon (add-stock) in June, July, August, and September, 1961. Length ranges of the fish, in inches, were 8.5–10.9 in Sigma, 8.3–10.8 in Tau, and 7.7–10.4 in Upsilon.

Food Organisms		*Total Number of Items, All Stomachs*			*Percent of Occurrence All Stomachs*		
		Sigma[a]	Tau[b]	Upsil[c]	Sigma[a]	Tau[b]	Upsil[c]
AQUATIC INSECTS							
Ephemeroptera							
Nonburrowers	nymphs	14	426	33	35.5	47.5	35.0
Burrowers	nymphs[d]	61	59	55	54.0	30.0	27.5
	adults[d]	0	6	0	0.0	5.0	0.0
Odonata							
Zygoptera	nymphs	9	157	0	20.8	37.5	0.0
	adults	42	0	0	2.5	0.0	0.0
Hemiptera							
Notonectidae	adults	0	0	2	0.0	0.0	5.0
Corixidae	adults	5	11	4	12.8	20.0	7.5
Coleoptera							
Haliplidae	larvae	0	1	0	0.0	2.5	0.0
	adults	1	0	0	2.8	0.0	0.0
Dytiscidae	larvae	1	1	0	2.5	2.5	0.0
Trichoptera	larvae	146	40	116	27.5	15.0	25.0
Diptera							
Culicidae	larvae	0	0	1	0.0	0.0	2.5
Tendipedidae	larvae	432	5	71	47.5	7.5	30.0
	pupae	438	65	28	20.0	15.0	25.0
	adults	4	4	1	7.5	5.0	2.5
Ceratopogonidae	larvae	4	0	2	10.3	0.0	5.0
OTHER AQUATIC ORGANISMS							
Cladocera		903	2,246	3	7.5	25.0	2.5
Ostracoda		360	783	0	2.5	10.0	0.0
Decapoda		6	9	5	13.3	10.0	12.5
Hydracarina		14	1	0	17.5	2.5	0.0
Pisces		0	1	1	0.0	2.5	2.5
TERRESTRIAL INSECTS							
Coleoptera	adults	0	2	15	0.0	2.5	5.0
Diptera	adults	1	0	2	2.5	0.0	2.5

[a] Thirty-nine stomachs examined, 37 of which contained food.
[b] Forty stomachs examined, 39 of which contained food.
[c] Forty stomachs examined, 29 of which contained food.
[d] Probably all *Hexagenia limbata* (Serville).

order of volume, the six ranked 1) crayfish, 2) burrowing mayfly nymphs, 3) nonburrowing mayfly nymphs, 4) caddis fly cases, 5) damselfly nymphs, and 6) midge larvae. On the basis of both categories, nymphs of large burrowing mayflies were the most frequent and important food item, followed by the nymphs of the smaller mayflies. Nymphs of both burrowing and nonburrowing mayflies were a prominent food item in all four months. Tendiped larvae were prominent in July only and of quite moderate occurrence in other months. Damselfly nymphs were a common item in August and quite scarce in other months. The cases of caddis flies were quite common in stomachs collected in both July and August, but were absent in those taken in June and September. Cladocerans occurred in nine of the ten stomachs taken in June, in only two in

July, and in one each in August and September. While young smallmouth bass were preyed upon when available, and their numbers frequently decimated, their remains were found in only two stomachs (one each in July and August), and on this basis they must be considered an item of minor importance. Scuds were not present in these ponds in 1961, but were undoubtedly a major food item following their establishment in 1963.

While a large proportion (88 percent) of the stomachs contained food, average volumes were small. In the control pond Sigma, 37 of 39 stomachs contained food, with an average volume for the 37 of only 0.49 milliliters. In the cropped pond Tau, 39 of 40 stomachs contained food, with an average volume of 0.39 milliliters. In the add-stock pond Upsilon, only 29 of 40 contained food, with an average volume of 0.92 milliliters. However, the picture of comparative volumes was distorted by two occurrences of comparatively large volumes of crayfish. If we remove crayfish volumes from the calculations, we then have averages of 0.25 in the control pond, 0.34 in the cropped pond, and only 0.12 in the overstocked pond. Though possibly fortuitous, these averages conform with the expected, where volume of food in stomachs was greatest in the cropped pond having the fewest fish, and smallest in the add-stock pond having a more dense population.

Review and Discussion of Smallmouth Bass Data

A survey of the literature revealed records of only five standing crops of smallmouth bass when maintained as a single species (Table 15). Maximum previous poundages were recorded by Regier (1962) from mark and recapture estimates made in a 0.09-acre pond in New York. These were at rates of 143, 146, and 139 pounds per acre over 3 consecutive years. The author observed that successful reproduction occurred in each of the 3 years, in spite of what he thought were high standing crops. Our three largest standing crops ranged from 169 to 180 pounds per acre (Unit 1 ponds), and our populations also reproduced successfully in all 3 years of census. While numbers of young-of-the-year surviving until fall in our three populations were in some cases small (188, 889, and 23), it should also be observed that none of our three populations was cropped to any substantial degree (maximum in any year: 8.4 pounds). Cropping of adult fish would be expected to enhance both reproductive success and survival of young, particularly when the populations were dominated by older and larger fish, as was true in both Regier's populations and ours.

Bennett and Childers (1957) recorded the next highest standing crop of 100.3 pounds (not including Age O) in a 1.4-acre gravel pit pond of "below medium" fertility in central Illinois. In the four years preceding the final census of this pond in June, 1955, it had produced successive hook-and-line yields ranging from 78 to 123 pounds per acre. The catches of 119 and 123 pounds per acre, made in 1952 and 1953 respectively, both exceeded the standing crop measured in 1955, and the authors believed this indicated that there was an annual replacement of fish flesh in this pond which exceeded the standing crop that the pond could support.

Our smallmouth populations produced no tangible evidence of a replacement potential of this species comparable to that provided by Bennett & Childers. We believe that this failure was due in part to the relative immaturity of our populations, to severe overcropping in at least one instance, and partly to chance. Our first cropped population (in Gamma, 1958–1959) had been initiated in May, 1958, with only 10 adults and 40 fingerlings, and in 1959 was so heavily cropped that too few fish remained to replace the flesh of those

Table 15. — Known published records of standing crops per acre of single species fish populations in small ponds.

Location	Method of Census[a]	*Standing Crop, Pounds Per Acre*				*Author*
		Bluegills	Largemouth Bass	Smallmouth Bass	Black Bullheads	
Kentucky	M & Ro	315.0				Turner, William R. (1959)
"	"	328.0				"
"	"	664.0				"
Oregon	M & R	89.7				Isaac & Bond (1963)
"	"	231.6				"
"	"		62.0			"
Texas	D		94.1			Brown, W. H. (1951)
"	"		76.2[b]			"
"	"		50.3[b]			"
Alabama	"		32.9			Swingle, H. S. (1952)
Illinois	"		48.2			Bennett, George W. (1954)
"	Ro			100.3		Bennett & Childers (1957)
New York	M & R			143.0 [c]		Regier, Henry A. (1962)
"	"			146.0		"
"	"			139.0		"
"	"			46.0		"
Iowa	Ro				288.0	Carlander & Moorman (1956)
"	"				128.0	"
"	"				653.0	"
"	M & R				134.3	"

[a] Symbols: M & Ro = marked and rotenone, M & R = marked and recaptured, D = drained, and Ro = rotenone

[b] Pond was fertilized.

[c] Same pond.

removed. We attempted to correct this situation in our next populations with initial stocks in Beta, Gamma, and Delta having weights ranging from 90 to 97 pounds. By unfortunate chance, however, the pond cropped during this experiment (Delta) simply did not have the productive potential to replace the weight of the fish that were cropped. Our third and last population to be cropped was that in pond Tau. A combination of overcropping of larger fish, and limited recruitment of younger fish (limited survival of young in 1961 and 1962, and no survival in 1963) left too few individuals to make an efficient conversion of available food. We therefore believe that the replacement potential of smallmouth bass in our ponds was not adequately tested.

Our oldest populations had completed three growing seasons when censused. Regier's data cited was from a population in its 6th, 7th, and 8th years, and the population studied by Bennett and Childers was in its 8th year when censused in 1955. All of these populations contained young-of-the-year when censused, and the heavily cropped population of Bennett and Childers had a normal composition, consisting of an estimated 5,000–6,000 young-of-the-year, 243 ranging in lengths of from 4 to 8.5 inches, and 49 fish longer than 10 inches. It should also be mentioned that none of these ponds received fertilization, which would have increased production. Strong evidence therefore exists that the smallmouth bass is capable of high, sustained yields when maintained as a single species in warmwater ponds.

LARGEMOUTH BASS

Bass used in these studies were obtained mostly from private ponds, partly from a state hatchery, and partly from a public reservoir, all located within the northern half of the state.

Data presented here were obtained over two periods of approximately one and one-half growing seasons each (1958–1960) in Unit 2 ponds, and from a 3-year period (1961–1963) in Unit 1 ponds. Ponds Zeta, Theta, and Iota (Unit 2) were completed and first filled with water in the spring of 1958. Each pond was stocked with 10 adults 10–13 inches long in May, and with a total of 61 subadults over the period June through August, for a total in each pond of about 16 pounds. In this series, pond Zeta was the control, pond Theta was cropped, and pond Iota received additions of stock.

In July, 1959, largemouth bass in all Unit 2 ponds were found to be severely infested by a gill parasite, *Dactylogyrus* sp. Since it would be extremely difficult to measure or evaluate the extent of deaths due to the parasites, it was decided to census the ponds before mortalities became a serious factor. On July 27, all three ponds were treated with rotenone. Based on returns of marked fish, the recoveries were judged to be comparable and reasonably complete in all ponds.

Following drainage and spraying of residual pools with a solution of HTH (available chlorine 15 percent), the ponds were refilled and restocked by August 25. Each pond was stocked with 514 young-of-the-year largemouths, plus an assortment of yearlings and adults to a total of approximately 30 pounds. The ponds were next drained in October, 1960.

The 1960 drainage censuses revealed the only notable contamination by unwanted species that occurred throughout these investigations. Pond Zeta contained three adult bluegills and an estimated 15–20 pounds of young-of-the-year bluegills. Pond Theta contained a single white crappie. Pond Iota contained two adult bluegills and between one and two pounds of young bluegills. The impact of these contaminants is believed to have been small. Other things being equal, the most likely influence would probably have been an increase in condition of bass in proportion to the degree of contamination. There was, in fact, an inverse correlation. Pond Zeta, with the greatest contamination (15–20 pounds) contained bass with the poorest average condition (3.8) in the three ponds, and pond Theta, with only the single adult white crappie contaminant had the best-conditioned bass (4.5). There are, however, additional considerations. Cropping from Theta would be expected to cause the remaining bass to have a higher rate of condition than bass in the uncropped ponds, which it seems to have done. At the least, then, we may say that the influence of the contaminants was not such as to have masked the effects to be expected from cropping. In the remaining analyses we have assumed the influence of the contaminating fishes to have been negligible though this may not have been strictly true.

Following the draining censuses of the Unit 2 ponds in October, 1960, the bass were regrouped by size and age and stocked in Unit 1, with supplemental stock added from other local sources. The ponds in Unit 1 had just been refilled following the draining censuses of smallmouth populations previously described.

Standing Crop Data

Table 16 presents standing crops in pounds per acre as measured by draining censuses of 11 populations of largemouth bass. The data are arranged according to experimental treatments given the populations, with an average standing crop presented for those ponds receiving identical treatments. Table 17 presents the same standing crop data

Table 16. — Standing crops in pounds per acre of largemouth bass in ponds receiving different experimental treatments. All censuses were by pond drainage on the dates or seasons indicated.

Unit	*Pond*	*Number of Growing Seasons*	*Date or Season of Census*[a]	*Standing Crop in Pounds Per Acre by Treatments Received*		
				Control	Cropped	Add-stock
2	Zeta	1½	7/27/59	21.7	..	..
2	Theta	1½	7/27/59	..	21.7	..
2	Iota	1½	7/27/59	..	..	37.6
2	Zeta	1½	F 1960	49.6	..	..
2	Theta	1½	F 1960	..	47.4	..
2	Iota	1½	F 1960	..	..	71.7
1	Beta	1	F 1961	126.8	..	..
1	Beta	2	F 1963	87.4	..	..
1	Gamma	3	F 1963	..	84.2	..
1	Delta	1	S 1962	..	..	120.6
1	Delta	2	F 1963	..	..	160.2
			Average	*71.4*	*51.1*	*97.5*

[a] Symbols: F = fall, S = spring.

together with such pertinent supplementary data as pounds originally stocked, pounds added to or removed from the population during the course of the experiment, and the net loss or gain in pounds of fish flesh by the termination of the experiment. Table 18 presents those standing crops obtained by estimation procedures in the spring in addition to those obtained by draining censuses in the fall, for ponds Beta, Gamma, and Delta. Original stock, computations of pounds lost or gained, and other supplementary data in Table 18 were derived or computed from figures obtained from the next previous census, whether it was by estimation or actual count.

Table 19 presents the numbers in each size or age group and percents of total numbers and weights of each group recovered in each draining census. Size and age separations in these censuses were less complete than those earlier made for smallmouth because of the multiple sources of stock and the degree of overlap between age groups.

Standing crops of largemouth in Unit 2 ponds ranged from a high of 71.7 pounds in the add-stock pond Iota in 1960 to lows of 21.7 pounds in both the control (Zeta) and cropped (Theta) ponds in 1959, all following approximately one and one-half seasons of growth. Standing crops in Unit 1 ponds ranged from a high of 160.2 pounds in the add-stock pond Delta in 1963 to a low of 84.2 pounds in the cropped pond Gamma in the same year. As in the smallmouth experiments, causes for variation included 1) the differences in experimental treatments received, 2) differences in pond fertilities, and 3) differences in size and/or age compositions of the populations. The effects of the experimental treatments are discussed quite fully in the text to follow. Without exception, however, standing crops among contiguous ponds within the same experimental units were highest in the ponds which received additions of stock, lowest in those from which fish were cropped, and intermediate in those ponds which were maintained as controls.

Unit 1 ponds, with basins of black dirt and clay, were much more productive than ponds in Unit 2 where bottoms were composed largely of sand overlayed with a blanket of clay. The visi-

Table 17. — Pounds of largemouth bass per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Zeta, Theta, Iota, Beta, Gamma, and Delta for periods of 1, 1½, 2, and 3 years. Censuses of ponds Zeta, Theta, and Iota in July, 1959, were by use of rotenone; all other censuses were made by pond drainage.

Unit	*Pond*	*Treatment*	*Date or Season of Census*[a]	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
2	Zeta	Control	7/27/59	1½	16.0	21.7	0.0	2.2	+ 7.9
2	Theta	Cropped	7/27/59	1½	16.3	21.7	0.0	24.6	+ 30.0
2	Iota	Add-stock	7/27/59	1½	15.1	37.6	23.0	3.1	+ 2.6
2	Zeta	Control	F 1960	1½	29.6	49.6	0.0	3.5	+ 23.5
2	Theta	Cropped	F 1960	1½	32.4	47.4	0.0	34.6	+ 49.6
2	Iota	Add-stock	F 1960	1½	30.2	71.7	33.6	0.0	+ 7.9
1	Beta	Control	F 1961	1	87.3	126.8	0.0	1.3	+ 40.8
1	Beta	Control	F 1963	2	105.7	87.4	18.2	3.6	— 32.9
1	Gamma	Cropped	F 1963	3	93.1	84.2	1.5	148.8	+138.4
1	Delta	Add-stock	S 1962	1	96.7	120.6	49.6	1.2	— 24.5
1	Delta	Add-stock	F 1963	2	120.6	160.2	100.5	4.6	— 56.3

[a] Symbols: F = fall, S = spring.

Table 18.—Standing crops of largemouth bass in 1-acre ponds Beta, Gamma, and Delta and pertinent supplementary data, as determined by draining censuses (exact count), or Petersen estimates, in spring and fall.

Pond	Season and Year of Census[a]	Type of Census	Number of Growing Seasons	Standing Crop, Pounds Per Acre	Pounds of Original Stock	Pounds Added	Pounds Removed	Pounds Lost or Gained
Beta	F 1961	Drainage	1	126.8	87.3	0.0	1.3	+ 40.8
Beta	F 1962	Estimate	1	124.7	105.7	18.2	2.9	+ 3.7
Beta	F 1963	Drainage	1	87.4	124.7	0.0	0.6	— 36.7
Gamma	F 1963	Drainage	3	84.2	93.1	1.5	148.8	+138.4
Delta	S 1962	Drainage	1	120.6	96.7	49.6	1.2	— 24.5
Delta	F 1962	Estimate	1	164.5	120.6	66.5	3.9	— 18.7
Delta	S 1963	Estimate	0[b]	128.1	164.5	0.0	0.0	— 36.4
Delta	F 1963	Drainage	1	160.2	128.1	34.0	0.7	— 1.2

[a] Symbols: F = fall, S = spring.

[b] There was no intervening period of growth between this spring estimate and that of the preceding fall. The deficit of 36.4 pounds in the pounds gained or lost column therefore indicates the estimated loss to overwinter mortality.

ble differences were the density of aquatic plants and the richness of the invertebrate fauna. The consequent differences in fish production are expressed by differences in standing crops in the control ponds of each unit. Maximum for a control pond in Unit 2 was 49.6 pounds per acre in Zeta in 1960, as compared to a maximum of 126.8 in pond Beta in 1961 (Table 17).

Fertilities of individual ponds within units were thought to be quite similar. This, for Unit 1, represented a marked change since the earlier period when rates of productivity and spawning success of smallmouth decreased in relation to their position in the flow series, i.e., from Beta to Gamma to Delta. During the summer of 1960 a water system was completed which permitted individual filling of each pond. With this new water system, productivities tended toward equalization. There was, in fact, some evidence that pond Delta, the least productive for smallmouth, may have had a narrow superiority in the production of largemouth.

The premature census of ponds in Unit 2 due to parasitism might be considered fortuitous, for it resulted in two sets of data rather than the intended one. Although the 1959 censuses occurred in July and the 1960 censuses in October, each period involved approximately one and one-half growing seasons, and the two are compared on that basis. A further difference was that the 1959 censuses were accomplished with rotenone, and those in 1960 by drainage. The clarity of the water and the high returns of marked individuals indicated a high recovery of the poisoned populations.

There is evidence that all populations in Unit 2 attained or exceeded the carrying capacities of their respective ponds under conditions which existed at times of census. Although the standing crops were quite small, particularly in 1959, it was verified that a potential for gain existed in these ponds by the surplus productions of 30 pounds in cropped Theta in 1959, and 49.6 pounds in the same pond in 1960. Larger gains would have been expected in the uncropped ponds if the carrying capacities had not been attained. Additional conclusions seem warranted by the almost perfect correspondence between the various quantities in the two different periods. In both study periods standing crop was highest in the add-stock pond and approximately equal in the control and cropped ponds; and surplus produc-

Table 19.—Numbers in each age or size group, and percents of total numbers and weights of each group in censused populations of largemouth bass in ponds Zeta, Theta, and Iota (Unit 2), and in ponds Beta, Gamma, and Delta (Unit 1), in years indicated.

Pond, Year of Census, Treatment[a]	*Total Number Censused in Each Age or Size Group*			*Percent of Total Number Censused in Each Group*			*Percent of Total Weight Censused in Each Group*			*Total, All Age Groups*	
										Number	Pounds
	Age 0	*Age I & Older, Less Than 10" Long*	*Age I & Older, 10" or Longer*	*Age 0*	*Age I & Older, Less Than 10" Long*	*Age I & Older, 10" or Longer*	*Age 0*	*Age I & Older, Less Than 10" Long*	*Age I & Older, 10" or Longer*		
Z 1959 0	103	59	7	61	35	4	4	78	18	169	21.7
T 1959 —	923	84	3	91	8	1	41	49	10	1,010	21.7
I 1959 +	319	122	8	71	27	2	8	78	14	449	37.6
Z 1960 0	32	191	24	13	77	10	3	57	40	247	49.6
T 1960 —	683	93	9	87	12	1	49	31	20	785	47.4
I 1960 +	20	262	48	6	79	15	1	44	55	330	71.7
	Age 0	*Age I*	*Age II & Older*	*Age 0*	*Age I*	*Age II & Older*	*Age 0*	*Age I*	*Age II & Older*		
B 1961 0	1,705	0	122	94	0	6	44	0	56	1,827	126.8
B 1963 0	203	54	189	46	12	42	3	8	89	446	87.4
G 1963 —	10,601	1	49	99	tr	1	61	tr	39	10,651	84.2
D 1963 +	363	0	388	48	0	52	2	0	98	751	160.2

[a] Ponds are designated as: Z = Zeta, T = Theta, I = Iota, B = Beta, G = Gamma, and D = Delta. Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.

tion was significantly high in the cropped ponds, intermediate in the control, and lowest in the add-stock ponds. It also seems significant that in both instances surplus production in the cropped pond exceeded final standing crop in the control pond. The consistent similarities suggest that the effects of the experimental procedures were valid and reasonably free from additional unrecognized influences. If true, we then had a valid expression of the relationship of total production to rate of cropping or exploitation wherein cropping stimulated growth, reproduction, and/or survival in the residual population with the consequence of an increased total production. In 1958–1959, surplus production (pounds gained) in the cropped pond was approximately 3.8 times that of the control pond; and in 1959–1960, it was about 2.1 times that of the control pond.

It is interesting to speculate as to whether the standing crops might have been the same in pond Theta with or without cropping. It may be that we were achieving an optimum rate of turnover for this population, and that the additional production was a "bonus" stimulated by an optimum cropping rate.

If we assume final standing crops to have approximated carrying capacities, as interpreted here, carrying capacity appears to have approximately doubled in the period from July 1959 to October 1960. While parasitism probably depressed growth to some degree in 1959, the greater production of fish in 1960 was believed due primarily to an increase in available food, principally crayfish.

In our second series, ponds Beta, Gamma, and Delta (Unit 1) were inventoried by both drainage and Petersen estimation procedures. As shown in Table 18, the control pond Beta was inventoried by a draining census at the end of the first growing season, by Petersen estimate at the end of the second, and by draining census at the end of the third. Our intimate knowledge of this population, based on frequent sampling, indicated that the 1962 estimate was within acceptable limits. If we accept this estimate we find that the standing crops were almost identical at near 125 pounds per acre in October of both 1961 and 1962, but dropped rather unaccountably to 87.4 pounds in October, 1963. The surplus productions in 1961 and 1962 were 40.8 and 3.7 pounds, respectively, being either moderately high or low as necessary to attain the presumed maximum. That these gains were not larger probably indicates that the standing crops in 1961 and 1962 approximated the carrying capacities of the pond at the times of census. These standing crops greatly exceeded those for largemouth bass measured in Unit 2 (Table 17), but were considerably below those of 170–180 pounds of smallmouth bass recovered from this pond (Beta) in earlier years.

Following the 1961 draining census, pond Beta was restocked with 105.7 pounds of bass, as shown in Table 18. The loss (pounds lost) of 36.7 pounds by October 1963 indicates that 1) the carrying capacity of pond Beta declined significantly during its third season, or 2) that the 1963 population was less efficient than those of 1961 or 1962. Decrease in standing crop implies a loss of efficiency by the population, or a decrease in available food. While no quantitative comparisons can be made, there was no evidence of a decline in available food. On the other hand, differences in population structure in the 3 years suggested possible differences in efficiencies of conversion of available food. From 1961 through 1963, progressively higher percentages of total weights were to be found in the larger sizes of bass. For example, in October 1961, 56 percent of the population (by weight) was made up of fish more than 8.5 inches long (Age II and older), while by October 1963, nearly 90 percent of the total weight of the population was represented by fish longer than 8.5 inches, most of which were now Age III or older. While an abundance of food may have been available for small bass in 1963, it possibly went largely unutilized because of the relative scarcity of small bass. With a more optimum size distribution of fish, the standing crop of pond Beta probably would have been higher. The obvious trend was a progressively greater depletion of small bass through predation by a progressively increasing proportion of larger bass. Had the larger bass been cropped by fishing the population would have assumed a more optimum composition and total production undoubtedly would have been higher. As previously observed, largemouth bass of larger sizes (in this case 8.5 inches and above) seem to lack the ability of smallmouth of similar sizes to forage for invertebrate foods, and are more dependent upon fish or other large food items.

For the cropped pond Gamma we have only the single final inventory of this population plus records of original stock and pounds cropped over the 3-year period. The total of about 148.8 pounds in the "pounds removed" column (Table 17) includes 31.04 pounds cropped in 1961, 81.34 pounds in 1962, and 36.40 pounds in 1963. In retrospect, it now appears that the removal of 81.34 pounds in 1962, followed by a cropping of 36.40 pounds in 1963, may have been excessive. While it caused accelerated growth and improved condition among the survivors, it left too few individuals of larger sizes to permit replacement of the pounds removed. This seems evident because the final standing crop was low as compared with those of companion ponds, and was comprised of 61 percent Age O fish by weight, and only 50 individuals older than Age O. The final standing crop included only one fish in the Age I group, and only six fish in the 6.5–9.5-inch length range. We thus created quite the opposite condition of that found in the uncropped pond Beta. In that first instance we had an excessive number of slow-growing, poorly conditioned older fish (243 Age I or older) comprising about 97 percent of the population by weight, as compared with too few, faster-growing older fish (50 Age I or older) comprising about 39 percent of the population weight. In each instance, production was limited, and final standing crop was less than the carrying capacity of the pond due to an imbalance in population structure.

The add-stock pond Delta was inventoried by a draining census in the spring of 1962, by Petersen estimates in the fall of 1962 and the spring of 1963, and again by draining census in the fall of 1963 (Table 18). There is a reasonable probability that the estimates are usable because 1) both mark-and-recapture samples were large (probably equalling or exceeding 50 percent of the total population), 2) the estimates were credible when compared with known numbers stocked and numbers later recovered by draining census, and 3) estimates of standing crops made in the spring and fall agreed closely with those obtained by actual measurements (draining censuses) at the same seasons in other years. On the basis of experiments conducted to evaluate the estimates (Buck & Thoits 1965), such errors as existed probably would have been negative.

If we are to accept these estimates, certain inferences may be drawn:

(1) Standing crops in all inventories of pond Delta at least equalled and probably exceeded carrying capacities. This seems evident from the fact that all quantities in the pounds gained or lost columns are negative (Table 18), indicating that the additions of stock had overtaxed available resources.

(2) Overwinter mortalities were large and fall carrying capacities exceeded those for spring. This seems apparent because standing crops inventoried in the fall exceeded those obtained

in the spring by approximately 44 pounds in the first instance and approximately 32 pounds in the second. Since pounds were lost in all instances, we believe that the carrying capacities at times of censuses were probably close to, but possibly somewhat below, the figures for standing crops. As in Unit 2, surplus production was highest in the cropped pond, intermediate in the control pond, and lowest in the add-stock pond.

Effects of Cropping on Fish Production

The influence of cropping on fish production is best illustrated by referring again to Table 17 which features the figures on "pounds lost or gained." The data from ponds in Unit 2 (Zeta, Theta, and Iota) are most rewarding. The significant points in the data are that 1) in both periods of observation, standing crops of largemouths in the control and cropped ponds were similar, 2) in both periods surplus production in each cropped population equalled or exceeded the final standing crop in both cropped and control ponds, and 3) surplus production in the cropped pond was 3.8 times that of the control pond in 1958–1959 and 2.1 times that of the control pond in 1959–1960. The combination of these data indicate that we here approached the optimum rate of cropping for these populations and that the replacement of fish flesh during each period was approximately the same as the ponds could support at any one time (100 percent).

Data from the Unit 1 ponds were less precise. The fact that the final "pounds gained" figure of about 138 pounds made in the cropped pond was so much larger than the amounts of the companion ponds indicated that cropping did indeed stimulate production. This, however, was an accumulated gain over three seasons, which translates to an average gain of approximately 46 pounds for each of the 3 years. We may note that the final standing crop of 84.2 pounds in this cropped pond was lower than that for either companion pond, and was comprised of a larger number (10,601) of young-of-the-year with only one fish of Age I and 49 that were of Age II or older (Table 19). The total of about 148.8 pounds cropped from this pond (31.04 pounds in 1961, 81.34 pounds in 1962, and 36.40 pounds in 1963) may have represented overcropping, particularly among fish of larger sizes. A more optimum distribution of sizes in this population — specifically, fewer fish of Age O and more of Age I —would undoubtedly have increased its potential for replacement of the fish flesh that was removed.

Growth and Condition

Table 20 presents growth data for fish of known age in the final censuses of 10 of our populations of largemouth bass along with growths made in other waters. Precise growth data for largemouth in ponds Zeta, Theta, and Iota were limited because of the variety of origins, sizes, and ages in the original stock, and because small confidence was placed in the interpretation of scale samples collected. The data in Table 20 are, therefore, limited to first-year growths made in these ponds. For other purposes, however, we used length frequency distributions to make the less precise separations presented in Table 21, and these provide limited additional information on growth in these waters.

Growth rates listed for 1959 were those which were terminated at the time of the premature census on July 29. First-year growths over the full 1960 season ranged from 4.3 inches in Theta to 4.8 inches in Zeta, and these were quite intermediate to first-year growths made in other waters with which they are compared (Table 20).

The 1959 section of Table 21 shows numbers of fish within four different size ranges in the populations censused in July, 1959, the average condition for each size grouping, and a designation

Table 20. — Growth of largemouth bass in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on largemouths in several other waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
Unit 2[a]	Zeta	1959	Control	2.6 (103)	..	..	..
	Theta	1959	Cropped	2.8 (923) [b]	..	..	..
	Iota	1959	Add-stock	2.7 (319)	..	..	..
Unit 2[c]	Zeta	1960	Control	4.8 (32)	..	..	..
	Theta	1960	Cropped	4.3 (683)	..	..	..
	Iota	1960	Add-stock	4.4 (20)	..	..	..
Unit 1[c]	Beta	1961	Control	4.1 (1,705)	..	..	..
	Beta	1963	Control	2.9 (203)	6.7 (54)	8.6 (152)	11.7 (37)
	Gamma	1963	Cropped	2.2 (10,601)	7.5 (1)	10.3 (40)	12.8 (8)
	Delta	1963	Add-stock	2.9 (363)	.. (0)	8.7 (221)	10.8 (167)
Other Waters	*Author*						
Oklahoma Reservoirs[d]	Jenkins & Hall (1953)			5.48	9.66	12.5	14.91
Norris Reservoir[d]	Stroud (1948)			6.9	12.2	14.7	16.1
Pennsylvania Pond[e]	Cooper *et al.* (1963)			3.5	3.98	..	..
Pennsylvania Pond[e]	Cooper *et al.* (1963)			5.25	8.42	..	..
Johnson Sauk Trail Lake, Ill[f]	Rock (1966)			4.0	7.2	10.9	13.0
Ramsey Lake, Ill.[f]	Stinauer (1966)			4.3	8.8	11.3	13.7
Red Hills Lake, Ill.[f]	Price (1966)			4.7	7.7	10.5	11.9
Ridge Lake, Ill.[g]	Bennett (1954)			8.1	10.3	12.6	13.6

[a] From actual measurements of live fish on July 29, 1959.

[b] Growth to July 29 only.

[c] From actual measurements of live fish at end of growing season.

[d] Lengths back calculated from scales.

[e] Based on measurement of live fish of known age.

[f] Lengths were determined from analysis of scales, and represent averages of growths made in from 5 to 8 separate years.

[g] Age categories for fish of these lengths based on scale analysis and fin clips of bass marked for individual censuses.

of the age class to which a majority of fish within each size group probably belonged. Two trends are apparent in these data: 1) a decline in condition with increase in size of fish within the same population, more prominent in the control and add-stock populations, and 2) a strong relationship between condition and density of stock when comparing fish of the same age in different populations. Condition declined progressively from 5.7 for the Age O fish to 4.2 for the group comprising the largest individuals in pond Zeta, and from 5.1 to 3.6 for the same age groups in pond Iota. This relationship was absent in the cropped populations because of the greater densities of stock of the smaller sized fish and lesser densities in the groups of larger sized individuals, as a natural consequence of cropping. As one makes further comparisons between rates of condition and densities of stock of fish of the same age or size class in the three ponds, it is evident that, without exception, condition was poorest where numbers were greatest and vice versa. For example, numbers of Age O fish in the three ponds were 103, 319, and 923, and rates of condition for these groups were 5.7, 5.1, and 4.6, respectively.

The 1960 section of Table 21 presents similar data for fish censused in the same ponds during October, 1960. Conditions again ranged from poor to average by Bennett's (1948) standards, the low averaging 3.78 (rounded to

3.8) for 166 fish in the control pond, Zeta, and the high averaging about 5.2 for 9 fish of the oldest class in the cropped pond Theta. The tendency for increasing condition with increase in size of bass was present in these populations due in part to a change in shape as the bass become larger and in part to a greater abundance of food (notably crayfish) for larger fish in 1960 over that of 1959.

The correlation between strength of year-class and average condition in the respective ponds was also less apparent in the 1960 census. As an example, 166 fish of the "mostly Age I" category in pond Zeta had an average condition of 3.8, as compared to 4.2 for 233 fish of the same class in the add-stock pond. We may note, however, that average condition of all three of the oldest year-classes in 1960 ranked higher in the cropped than in either companion pond, due probably to their lesser abundance as a result of cropping. Transfer of better-conditioned fish from the cropped to the add-stock population could have contributed to the higher condition of certain age classes in pond Iota than in the control pond, but we believe the differences were due primarily to a slightly greater fertility of the add-stock pond.

Growth data of two types are also presented for largemouth from ponds in Unit 1 (Beta, Gamma, and Delta). Data presented for comparison with growths made in other waters (Table 20) are restricted to fish of known age, and represent an average of all fish in the final draining censuses for which ages were known. Additional growth data are presented in Fig. 4 where growth curves are based on samples collected during the months indicated.

As is evident in Table 20, growths in these single-species populations were slower than in most mixed populations with which they are compared, even in some instances when growth was stimulated by relatively heavy cropping.

Table 21.—Numbers of largemouth bass of various size and age groups in the 1959 and 1960 censuses of ponds Zeta, Theta, and Iota, with average coefficients of condition for each group.

Pond	Treatment	*Age 0*			*Mostly Age I*			*Mostly Age II*			*Age III or Older*		
		Number in Census	Length Range, Inches	Average Condition	Number in Census	Length Range, Inches	Average Condition	Number in Census	Length Range, Inches	Average Condition	Number in Census	Length Range, Inches	Average Condition
	1959												
Zeta	Control	103	2.0–3.1	5.7	18	6.1–7.7	5.4	41	8.0–9.9	5.0	7	10.5–12.3	4.2
Theta	Cropped	923	2.5–3.4	4.6	76	4.6–8.3	4.7	8	8.7–9.9	5.2	3	10.7–11.7	4.9
Iota	Add-stock	319	2.5–3.0	5.1	44	5.0–7.8	4.9	78	7.7–9.4	4.7	8	10.0–13.9	3.6
	1960												
Zeta	Control	32	4.0–5.2	4.6	166	5.8–7.9	3.8	25	8.0–9.9	4.0	6	10.0–13.9	4.5
Theta	Cropped	683	3.9–4.6	3.8	84	5.9–7.9	4.4	9	8.0–9.9	4.4	9	10.0–16.4	5.2
Iota	Add-stock	20	4.1–4.7	3.9	233	5.5–7.9	4.2	29	8.0–9.9	4.2	8	10.0–16.9	4.7

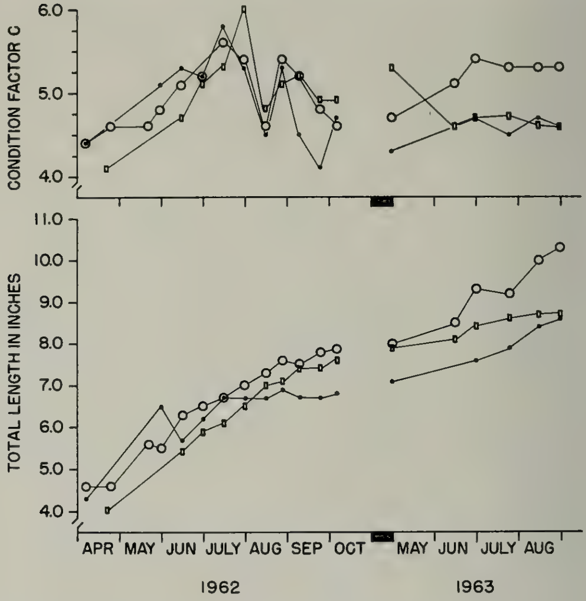

Fig. 4.—Growth and condition (C) of largemouth bass of the dominant 1961 year-class over the 1962 and 1963 growing seasons in the control pond Beta (dots), cropped pond Gamma (circles), and add-stock pond Delta (rectangles).

Cooper *et al.* (1963) demonstrated that heavy cropping of a population of yearling bass in a Pennsylvania pond caused substantial improvement in growth and condition, and in surplus production. It should be pointed out that the Pennsylvania study was a comparison of data from a single pond in different years while our comparisons were of data from different ponds in the same year. As emphasized earlier, differences in environments frequently masked the influences of our experimental treatments. While our rates of surplus production were consistently greatest in cropped ponds, and lowest in the add-stock ponds, rates of growth and condition showed less conformity.

Our most complete data comparing growth with condition are for the 1961 brood over the 1962 and 1963 growing seasons since this was the age group that was most abundant and the most heavily cropped over that period. Fig. 4 presents growth and condition curves for the 1961 year-class based on approximately bimonthly samples over most of the 1962 and 1963 growing seasons, with the terminal points in 1963 representing averages of all fish in the final censuses. Growth and condition curves are based on identical samples. After mid-June, 1962, the growth curve representing the cropped population ranked higher than that of either companion population and the margin of difference increased steadily throughout 1963.

Coefficients of condition computed from the same samples were extremely variable from one sampling period to the next throughout 1962, but all three populations exhibited similar patterns of seasonal variation. Condition in all ponds improved steadily from spring to a mid-summer peak, dropped sharply over the period from mid-July to mid-August, rose to a second but lower peak by early September, and then declined again. Differences in patterns between individual populations were not great in 1962, and showed little influence from the experimental treatment. In 1963, however, condition of the cropped population had achieved a distinct superiority by early June, and this was maintained throughout the 1963 season.

While the cropped population ranked high in both growth and condition in 1963 (Fig. 4), growth in the add-stock population was higher than, and condition was similar to, that in the control pond throughout much of both 1962 and 1963. Such an advantage in the add-stock population could have been influenced to the degree to which faster-growing, better-conditioned fish transferred from the cropped pond contributed to the samples obtained from the add-stock population. However, inspection of our samples showed that the transferred fish composed such a small part of the samples as to render their influence negligible. Faster growth and better condition of fish in the add-stock pond than in the control pond, in spite of the greater density of stock in the add-stock pond, were believed due to a higher productivity for the add-stock pond than for the control pond Beta. As mentioned before, this indicated a reversal in the comparative productivities of the two ponds since the earlier period with the stock of smallmouth bass.

The condition curves for our Age I fish in 1962 (Fig. 4) illustrate the degree to which the condition of such a population may fluctuate over short periods of time. The similarity of curves in all ponds suggests that the fluctuations were due to some natural phenomenon common to all ponds. Since our Age I bass were largely dependent upon zooplankton and other small invertebrate foods, the fluctuations were probably related to normal variations in the availabilities of these foods. The relative stability of the condition curves for these same fish when larger and one year older in 1963 suggests that they were then subsisting on larger food items of a more stable supply. This may well have been crayfish, or the 1963 spawn of bass, or both.

Fig. 5 shows rates of condition plotted against lengths of bass recovered from ponds Beta, Gamma, and Delta in the draining censuses of October 1963 and allows a comparison of the three curves

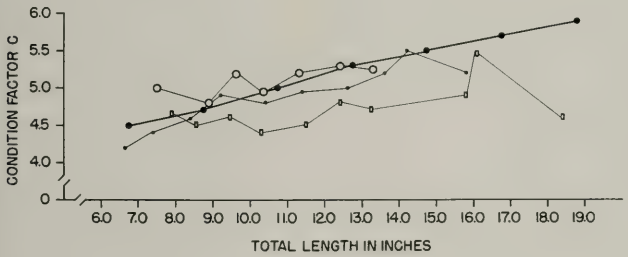

Fig. 5.—Coefficients of condition (C) in relation to lengths of largemouth bass for populations in the control pond Beta (small dots), cropped pond Gamma (circles), and add-stock pond Delta (rectangles) in 1963 compared with similar data (large dots) for bass from a mixed species population in an Illinois reservoir (Ramsey Lake: Stinauer 1966). Points plotted are the averages of condition for bass of convenient length groupings against the mid-length of each length grouping.

with a similar one for bass from a normal, mixed population from an Illinois reservoir (Stinauer 1966: Ramsey Lake). Conditions of our bass were commonly highest in the cropped pond, lowest in the add-stock pond, and intermediate in the control pond. While our bass showed a common though slight tendency for increased plumpness with increase in length, the tendency was less marked than in the normal population with which they are compared. This tendency may be typical of single-species populations of bass having no companion fish as a source of forage.

Mortalities

Rates of mortality for largemouths in ponds, Zeta, Theta, and Iota were poorly known because of incomplete knowledge of year-class strengths. Information is limited to those fish which were marked and transferred from Theta to Iota or were marked and released where caught. Since ages were poorly known, they usually were designated only as "Age I and Older" or "Age II and Older." The limited data permit three general observations: 1) mortalities of those fish marked and transferred were consistently a little higher than for those resident fish marked and released in the same (add-stock) population, 2) mortalities in the add-stock populations were slightly higher than for fish in the less densely populated companion ponds, and 3) known rates of mortality for largemouth were not notably different from those for similar categories of smallmouth in ponds Beta, Gamma, and Delta in 1959–1960, insofar as they could be compared.

In 1960 we attempted a study of rates of seasonal mortality based on recoveries in fall draining censuses of fish given distinctive fin clips at earlier periods in the growing season. Numbers marked in each period, numbers recovered in the final censuses, and percents of mortality are presented in Table 22. Because the fish marked were of a variety of sizes, and not of a single age class as in the earlier, similar experiment with smallmouth bass, the range in length and average length of each lot of marked fish are included in the table. Mortalities by the end of the 1960 growing season ranged from a low of 27.3 for 22 fish marked in pond Zeta in August to a high of 69.2 for 13 fish marked in pond Iota in April. Averages of mortalities (all ponds combined) for bass marked in each month showed a decrease from 48.9 percent for all fish marked in April to averages of 38.4, 37.9, and 30.5 for fish marked in the months of June, July, and August respectively. When rates of mortality for all fish marked in each pond were averaged (all marking periods combined), mortalities in the add-stock population (44 percent) exceeded those in either companion pond (33.2 percent and 39.6 percent in Zeta and Theta respectively). As in our smallmouth experiments, all mortality rates were abnormally high. The data indicated a rather high and fairly uniform mortality due to handling and marking, with a slight increase in mortality with increase in time the fish were marked.

Table 22 also reveals that mortalities were quite uniform over the size ranges marked, and not greater for either smaller or larger (younger or older) fish. This was evident from the rather normal and consistently small differences between those average lengths, as well as ranges in lengths, that were determined when the fish were marked and when they were recovered. A disproportionately high mortality among older fish would have been reflected by a lesser average length for those fish recovered than for those marked, and greater mortality of smaller fish would have had the opposite effect. A comparison of the lengths in Table 22 indicates a range of differences that in most cases would represent normal growth increments.

Rates of mortalities of the largemouth population from Unit 1 are more completely known because of greater knowl-

Table 22.—Numbers and sizes of largemouth bass marked and returned to ponds Zeta (control), Theta (cropped), and Iota (add-stock) in various months in 1960, and numbers and sizes recovered in the fall draining censuses, with percents of mortality.

Month	*Number Marked and Returned, Number Recovered, and Percent Mortality*[a]			*Length Range and Average of Total Length in Inches*[b]					
				When Marked			When Recovered		
	Zeta	Theta	Iota	Zeta	Theta	Iota	Zeta	Theta	Iota
April	26 17 34.6	14 8 42.9	13 4 69.2	3.4–14.9 *7.3*	3.9–11.3 *7.7*	3.6–16.3 *7.1*	6.4–15.0 *8.9*	6.2–11.5 *10.0*	5.8–10.8 *8.5*
June	27 16 40.7	25 15 40.0	26 17 34.6	4.7–16.0 *9.0*	4.2–15.5 *9.1*	6.7–15.7 *9.9*	6.9–16.2 *10.3*	6.2–15.4 *10.2*	7.7–16.2 *10.9*
July	30 21 30.0	13 7 46.2	32 20 37.5	4.7–12.1 *6.6*	5.0–11.7 *7.3*	4.6–13.5 *6.7*	6.7–12.5 *8.1*	6.1–11.9 *8.4*	5.7–13.4 *7.8*
Aug.	22 16 27.3	41 29 29.3	23 15 34.8	5.6–11.3 *7.3*	5.3–16.0 *6.7*	5.3–15.2 *8.2*	6.2–11.4 *7.7*	5.5–15.9 *7.1*	5.9–15.2 *8.6*
Average Mortalities	*33.2*	*39.6*	*44.0*						

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[a] The sequence in each group of numbers corresponds to the order of categories as mentioned here; for example, in pond Zeta in April, 26 fish were marked and returned, 17 were recovered, and mortality was 34.6 percent.

[b] Total length averages are shown in italic.

edge of their age compositions. When possible, as during a draining census, entire year classes were given distinctive marks. These, plus marks given during normal sampling, and to fish transferred during each year, made it possible at times of census to compute rates of mortality for most components of the populations. Known rates of mortality for fishes stocked in or transferred to pond Delta are presented in Table 23.

Pond Delta contained 363 Age O bass when censused in October, 1963. This was particularly interesting since our observations had indicated no successful reproduction (and certainly no survival) in this pond in either previous year. We believe that the earlier failures were related to high pH levels, as discussed in the section devoted to spawning success.

Age I was completely missing in the 1963 fall census of pond Delta. The 1962 spawn had been unsuccessful, and the 451 Age O fish transferred from Gamma as 2–4-inchers in late August and September, 1962, had disappeared, probably through predation.

As indicated in Table 23, Age II fish (1961 year-class) in the final population of pond Delta contained four components for which mortalities ranged from 16.7 to 90.3 percent. Mortalities were higher among transferred than among resident bass and were highest among those fish transferred earliest and when smallest. We suspect, however, that higher mortalities were related more to the size of the fish when transferred than to length of time in the new population.

The Age III and older fish also had four separate origins. Mortalities (Table 23) ranged from 16.7 to 82 percent, and were again related to length of time in the population and/or to size of fish when transferred.

Known rates of mortality for bass in the control pond Beta are presented in Table 24, and are restricted to the original stock of October, 1960, or to those restocked following the draining census of October, 1961. A total of 1,705 young-of-the-year were recovered in the draining census of October, 1961, of which 892 were marked and restocked. The recovery of only 152 of this marked group in the census of October, 1963, indicated a mortality of 83 percent over the final 2-year period.

Table 23. — Mortalities of various categories of largemouth bass based on recoveries in the draining census of pond Delta (add-stock) in October, 1963.

Year Class or Classes	*Origin, or Number Originally Stocked*	*Recovery in Oct., 1963 of Bass Marked and Transferred to Delta in Year Indicated*	*Total Number Recovered*	*Percent Mortality*
1963	Spawned in Delta, 1963	. .	363	Unknown
1962	Spawned in Delta, 1962	. .	0	100.0
1962	Transferred from Gamma	0 of 451 (1962)	0	100.0
1961	581[a]	. .	132	77.3
1961	Transferred from Gamma	7 of 72 (1961)	7	90.3
1961	Transferred from Gamma	52 of 191 (1962)	52	72.8
1961	Transferred from Gamma	30 of 36 (1963)	30	16.7
1960 or Older	478[b]	. .	86	82.0
1960 or Older	Transferred from Gamma	27 of 72 (1961)	27	62.5
1960 or Older	Transferred from Gamma	34 of 70 (1962)	34	51.4
1960 or Older	Transferred from Gamma	15 of 18 (1963)	15	16.7

[a] Since no spawning was observed in 1961, all 1961 year-class fish not transferred to pond Delta are believed to have originated from this stock of 581 1-inch fry in mid-June, 1961.

[b] The 478 included 231 Age 0 fingerlings, 212 that were mostly of Ages I and II, and 25 that were mostly Ages III and IV when stocked in October, 1960, and 10 of Ages II and Older stocked in May, 1961.

Table 24. — Mortalities of various categories of largemouth bass based on recoveries in the draining censuses of pond Beta (control) in October, 1961, and October, 1963.

Year Class or Classes	*Number Originally Stocked*[a]	*Number Recovered in 1961*	*Percent Mortality*	*Origin, or Number Restocked in Oct., 1961*	*Number Recovered in 1963*	*Percent Mortality*
1963	..	..	..	Spawned in Beta, 1963	203	Unknown
1962	..	..	..	Spawned in Beta, 1962	54	Unknown
1961	585	1,705	Unknown	892	152	83.0
1960	132	0	100.0	..	..	..
1959 or Older	295	112	62.0	129	37	71.3

[a] Eight bass of the oldest group (1959 or older) were stocked in May, 1961, all 585 of the 1961 year-class were stocked as 1-inch fry in mid-June, 1961; all others (73.86 pounds) were stocked in October, 1960.

The remaining population was comprised of 37 older and larger individuals, none of which bore marks. Their origin traces back to the original stock of 295, nearly all released in October, 1960 as mixed Age I and older (mostly Age II and III). A total of 112 of these fish were recovered in October, 1961, representing a mortality of approximately 62 percent over the 12-month period. Seventeen fish of the same age were added to the group, bringing the total restocked in October, 1961 to 129. Our final total of 37 therefore represented a mortality of approximately 71 percent over the final 2-year period.

The original stock in the cropped pond Gamma numbered 1,014 individuals, including 585 fry of the 1961 brood, 132 fingerlings from the 1960 brood, and a total of 297 individuals that were Age II or older (mostly Age III and IV) in 1961. By time of final census in October, 1963, only 49 individuals remained of this original stock, including 40 of the 1961 year-class, none of the 1960, and only 9 individuals of the oldest group, by then Age IV or older. Of the 1961 brood, a total of 425 had been cropped over the 3 years. The total of the two figures (425 cropped plus 40 recovered = 465) implies a much higher survival than one would expect from an original stock of 585 1-inch fish, and a small survival of the 1961 spawn is indicated.

Of the 132 fingerlings in the original stock, none was cropped in any year, and none was recovered in the 1963 census. It seems likely that this age group was decimated quite early by predation.

Of the original stock of 297 older fish, 72 were cropped in 1961, 71 in 1962, and 18 in 1963, for a total of 161. Only 9 of this group were recovered in the 1963 census, which meant that 127 must have died natural deaths over the 3-year period.

The final 1963 standing crop in the cropped pond Gamma also contained 10,601 young-of-the-year, as compared to only 203 and 363 of the same age in the two companion ponds. This large survival of young was coupled with the recovery of only 49 fish older than Age I, as compared with totals of 189 and 388 fish of similar ages in the control and add-stock ponds respectively. Differences in surviving young were probably related to differences in numbers of older fishes and corresponding differences in predation.

Spawning Success

Successful spawns of largemouth bass occurred in ponds Zeta, Theta, and Iota (Unit 2) in all years, 1958 through

1960, and young-of-the-year were recovered in all draining censuses. Attempts to obtain comparative counts of schools of fry in ponds of both Units 1 and 2 were unsuccessful, due primarily to concealment of the fry by either large mats of filamentous algae or submerged aquatic weeds. As may be seen in Table 19, the numerical abundance of young-of-the-year in all final standing crops was much higher in the cropped than in the companion ponds. This may have reflected higher rates of spawning success due to lesser densities of breeding stock in the cropped ponds than in the companion ponds, as observed in the smallmouth populations, or may have been due to lesser degrees of predation by lesser numbers of older and larger fish in the cropped ponds, or both.

In Unit 1, successful spawns were known to have occurred in all ponds in all years, 1961–1963, except in pond Delta in 1961. A series of observations made in 1963 suggested a possible reason for the apparent failure in pond Delta in 1961, as well as for limited production of young in that pond in 1962. On May 9 and 10, 1963, adults were observed to be building nests in ponds Gamma and Delta but not in pond Beta. By early June, young-of-the-year had been seen in both Gamma and Delta, but neither young nor spawning activities of any type were observed in pond Beta throughout May or early June. During May we also observed that weeds of various *Potamogeton* spp., particularly *P. crispus* L., were becoming extremely dense in pond Beta, and considerably more so than in either companion pond. As an apparent consequence to the dense vegetation and associated high rates of photosynthesis, the pH of the pond waters rose to levels above 10.2 in pond Beta, and to levels of between 9.5 and 10 in ponds Gamma and Delta. Fish of larger sizes in pond Beta were observed to be extremely listless, with some appearing to be dazed and gasping for air at the surface, while at the same time smaller fish of about 8-inch lengths appeared unaffected. On May 27 approximately 1.25 acre-feet of fresh water were introduced into pond Beta, and the pH receded to about 9.5 and the fish appeared to recover. The treatment proved quite temporary, however, and we decided to eliminate the weeds to reduce the high pH. On June 4, 1963, approximately one-third of the area of each of the three ponds was treated with enough endothal to provide a concentration of about 1 ppm in each treated area. On the basis of total pond volumes, the concentrations were probably between 0.3 and 0.5 ppm. The treatments proved to be effective in all ponds. As the weeds began to die and the pH levels declined, the bass in pond Beta were observed to build nests and commence spawning activities. Nests were first observed on June 19 and 20, approximately 6 weeks later than in either companion pond, and several successful hatches were later recorded. We have attributed this delayed spawning to the high pH during the normal spawning season. From observations made in the three ponds we believe that the critical level of pH was in the range of 9.6–10. These observations agree closely with those made by Jackson (unpublished) in some Wisconsin hatchery ponds where he reported no successful reproduction by bass in those ponds in which the pH remained at 9.6 or above during the spawning season. While adult bass have been known to tolerate pH levels exceeding 10 for short periods (Doudoroff & Katz 1950), reproduction may be restricted at somewhat lower levels. We believe, as did Jackson, that high pH may influence bass production in one or more ways:

1. High pH may inhibit spawning.
2. High pH may kill the eggs or larvae.
3. Emerging fry may starve to death due to elimination of zooplankton by high pH.

Since levels of 9.6–10.2 were common to our new, poorly buffered ponds in earlier years, we suspect that high pH may have eliminated or seriously reduced spawning of bass in those years.

Review and Discussion of Largemouth Bass Data, and Comparison with Smallmouth Data

Brynildson & Truog (1959) have recommended the stocking of Wisconsin warmwater ponds with largemouth bass alone because of unsatisfactory results from combinations of bass and bluegill. Brynildson (personal communication) has reported fairly good fishing from such single species populations providing the bass are not eliminated by winterkill or lack of natural reproduction. Bass alone have been stocked fairly extensively in both Illinois and Oregon. Bennett (1962) has achieved satisfactory results in Illinois ponds by stocking an assortment of bass larger than 10 inches, in addition to 100 fingerling bass per acre. The adults produced young at the first spawning season after stocking, and the fingerlings already present prevented the development of a dominant new brood subject to stunting. Bond (personal communication) has reported excellent fishing in some Oregon ponds and poor results in others (particularly in small, weedless ponds) due to stunting and limited reproduction, and he believes that best results may be obtained from use of ponds with areas of 2 acres or more. In a series of fishing trials, Bond and his associates found bass fishing to be much superior in single species populations than in populations containing both bass and bluegill. Largemouth are known to have been stocked as single species in ponds in other localities, but few such populations have been evaluated, due probably to early contamination by other unwanted species.

A search of the literature has provided only six listings of standing crops of bass as a single species (Table 15). The maximum poundage reported was 94.1 pounds per acre in a small, unfertilized pond in Texas (Brown 1951). However, Mraz (1964) has reported data from a stunted population of largemouths in a 1-acre pond in Wisconsin where the standing crop appeared to have exceeded 200 pounds per acre. The author reported removing 688 bass 5–9 inches long, and weighing about 100 pounds, in a single seine haul in the fall. The pond was heavily fished by hook and line both prior to this removal and during the following summer. In the following fall an additional 707 bass were removed, having a total weight of 108 pounds and an average length of 7 inches, and which had made practically no linear growth during the year. A substantial population of small bass also remained following this second harvest. The data suggest that both harvests were from the same age and size class of bass, which means that the standing crop at the time of the first harvest must have exceeded 200 pounds per acre.

Our largest standing crop was 160.2 pounds per acre in pond Delta in October, 1963 (Table 17). However, this population had received heavy additions of stock (100.5 pounds) since the last previous inventory, and the deficit of 56.3 pounds in the "pounds lost or gained" column indicated that the pond's carrying capacity had been surpassed. The maximum poundage recovered from a control pond was 126.8 pounds per acre from pond Beta in October, 1961. This pond had received an original stock in the preceding October of 87.3 pounds, and upon drainage contained 1,705 Age O fish (55.6 pounds) ranging in length from 3 to 6.9 inches, no bass of Age I, and 122 bass (71.2 pounds) that were Age II or older, ranging from 8.5 to 18.6 inches in length. Additional inventories (Table 18) indicate that from 120 to 130 pounds per acre may have been the maximum carrying capacity of these ponds for largemouths. These compare with maximums of from 170 to 180 pounds of smallmouths earlier recovered from ponds in this same unit. Greater production of smallmouths than largemouths was believed due primarily to the superior ability of smallmouths of larger sizes to subsist on an invertebrate diet.

As observed in Oregon and Wisconsin, largemouth bass as a single species are sometimes self-limiting due to predation of young, or failures to reproduce. We observed a common tendency toward progressively greater proportions of older and larger fish in both smallmouth and largemouth populations, but elimination of young was less pronounced among largemouths than smallmouths in our studies. Table 25 compares the final compositions of 10 populations for each species (4 control, 3 cropped, and 3 add-stock populations). Higher average standing crops of smallmouth than largemouth bass were associated with greater numbers and greater percentages by weight of fish older than Age O in the final smallmouth than in final largemouth populations. For both species, numbers of fish older than Age O were highest in the add-stock ponds, lowest in the cropped ponds, and intermediate in the control ponds. One would suspect that numbers of Age O fish in the final censuses might be inversely correlated with numbers older than Age O. This was true for largemouth, but not true for smallmouth populations. Average numbers of young smallmouths were 422 in four control ponds, 582 in three add-stock ponds, and only 23 in three cropped ponds. Comparable figures for largemouths were 511 in four control ponds, 234 in three add-stock ponds, and 4,069 in three cropped ponds. It is not clear whether smaller numbers of Age O smallmouths than largemouths in the final censuses were due to the lesser fecundity of the smallmouths, to greater predation on smallmouth young by their elders, or to more periods of high pH. The greater numbers of older smallmouths could have accounted for greater predation. However, the fact remains that all populations of largemouths contained young-of-the-year at the times of the fall censuses, ranging in individual ponds from 20 to over 10,000 survivors (Table 19), and average numbers of these survivors were higher in largemouth than in smallmouth populations (Table 25). Evidence therefore exists that largemouths alone also are capable of sustained, year-to-year production in 1-acre ponds, especially when subjected to cropping.

Numbers of surviving young-of-the-year in cropped largemouth ponds aver-

Table 25. — Comparison of final compositions of 10 populations of largemouth bass with 10 of smallmouth bass on basis of treatments received. Averages are presented for four control, three cropped, and three add-stock populations for each species.

Species of Bass	*Type and Number of Populations Averaged*	*Average Standing Crop, Pounds Per Acre*	*Average Percent of Weight of Fish in Specified Age Group*		*Average Number of Fish in Final Census in Specified Age Group*		*Average Percent of Numbers of Fish in Specified Age Group*	
			Age 0	Older	Age 0	Older	Age 0	Older
SMALLMOUTH	Control (4)	93.4	5.8	94.2	422	207	43.7	56.3
	Cropped (3)	46.2	12.5	87.5	23	166	40.3	59.7
	Add-stock (3)	149.6	6.2	93.8	582	584	36.1	63.9
LARGEMOUTH	Control (4)	71.4	13.5	86.5	511	159	53.2	46.8
	Cropped (3)	51.1	50.3	49.7	4,069	80	92.6	7.4
	Add-stock (3)	89.8	3.7	96.3	234	276	41.8	58.2

aged much higher than in companion largemouth ponds, as seems normal and expected, but numbers of surviving young in cropped smallmouth populations averaged much less than in companion smallmouth ponds (Table 25). As mentioned previously, the apparent spawning failure of smallmouths in cropped pond Tau in 1963 may have been due to the absence of a breeding pair, or to predation of eggs or larvae by an abundant population of crayfish. We suspect that other failures of smallmouths in cropped ponds were related more to physical or chemical limitations in the environment, as discussed in the sections devoted to spawning success, than to any significant difference in behavior of the two species.

Ponds in Unit 2 provided evidence that under an optimum program of cropping, largemouth populations are capable of a seasonal replacement of fish flesh equal to the poundage that the pond can support.

Our most efficient largemouth populations were believed to be those comprised of large weights of both small and large fishes, and this division of sizes was apparently more critical in largemouth than in smallmouth populations. As detailed earlier, standing crops of largemouths in pond Beta declined substantially as the population progressed from an approximate equal division of weights of fishes of Age O and those of Age II and older to one in which about 90 percent of the weight was comprised of fish longer than 8.5 inches (Age II and older). Populations of smallmouths in these same ponds attained maximum poundages (170–180 pounds) when over 90 percent of the weights were comprised of fishes that were Age I and older in one instance and Age II and older in two instances. The essential difference apparently lies in the greater ability of smallmouth of larger sizes to make efficient use of invertebrate foods. Probably none of our bass populations attained the maximum of which either species was capable. While we have little knowledge of what constitutes an optimum size distribution, and it would probably vary with the type and amount of available foods, we would presume it to be one in which all sizes and ages of fish had optimum representation. Since even our most productive populations had one or more age (and size) classes missing, possibly none achieved maximum efficiency.

As noted for the smallmouth populations, carrying capacities for largemouths were larger in the fall than in the spring. As shown in Table 18, standing crops measured in pond Delta in the spring were 120.6 pounds (drain census, 1962) and 128.1 pounds (estimate, 1963), as compared with fall standing crops of 164.5 pounds (estimate, 1962) and 160.2 pounds (drain census, 1963) in the same pond. Thus, carrying capacities in pond Delta in the spring were approximately 77 percent as large as those in the fall.

Carrying capacities of ponds in Unit 2 showed a marked increase over the period 1958–1960, due primarily to increased production of crayfish and other invertebrates, but there was no evidence that the carrying capacities of ponds in Unit 1 increased over the period 1961–1963. However, carrying capacities were evaluated by differences in standing crops, and these were influenced by differences in size and age compositions of the populations. Thus, differences in population structures in the different years could have masked any increase in carrying capacities.

As in the smallmouth populations, life histories of the largemouths were strongly influenced by differences in population densities. In general, rates of growth and condition were poorest, and rates of mortality highest, in those populations having the greatest densities of stock. Again, however, fastest growth rates were not always accompanied by highest rates of condition, and comparative rates of either were sometimes poor indicators of comparative rates of the other. Comparative rates of reproduction were poorly known, but numbers of young-of-the-year surviving through their first growing season were consistently by far the highest in the cropped populations.

YELLOW PERCH

We will present data obtained over 2-year (1958–1959) and 1-year (1960) periods from the single pond Alpha, earlier devoted to smallmouth bass, and a 3-year period (1961–1963) in ponds Zeta, Theta, and Iota (Unit 2), which earlier contained largemouth bass. The original stock of perch was transported from the Green Bay section of Lake Michigan where the fish had been trapped by personnel of the Wisconsin Department of Conservation.

Pond Alpha was first stocked with perch on April 30, 1958, receiving 79 males and 4 females, all adults of unknown age, having a total weight of 19.4 pounds. In spite of a loss of eggs, in transportation, by one or more of the 4 females a substantial spawn was obtained. Cropping in 1958 consisted of only 20 young weighing about 1 pound. Total cropping in 1959 was 78.7 pounds, including 57.2 pounds removed by summer hook-and-line fishing, and an additional 21.5 pounds taken by wire traps in October. Following the October draining census in 1959 the entire population was replaced in the pond. This included two of the original adults, 1,531 young-of-the-year, and 464 yearlings, representing a combined total weight of 123.4 pounds. In addition, 21 adults from a local lake were added to augment the breeding population, which brought the weight of the original stock for the 1960 experiment to 125 pounds. The pond was cropped of a total of 88.3 pounds in 1960, and when censused in October of that year had a standing crop of approximately 192 pounds. Perch obtained from the 1960 census of pond Alpha were immediately restocked in ponds Zeta, Theta, and Iota, with each pond receiving 3,771 young-of-the-year and 225 of mixed Ages I and II for total weights in each of about 52 pounds. These populations were sampled and observed through three growing seasons (1961–1963), and final censuses were accomplished in October, 1963. Pond Zeta was cropped, Theta received additional stock, and Iota was maintained as a control.

Standing Crop Data

Table 26 presents standing crop data for six populations of perch together with such pertinent supplementary data as pounds of original stock, pounds added to or removed from the populations during the course of the experiments, and the net gain or loss in pounds of fish flesh by the termination of the experiment. Table 27 presents numbers in each size or age group and percents of total numbers and weights of each group recovered in each draining census.

Standing crops of perch ranged from a low of 51.3 pounds per acre in the cropped pond Zeta in 1963 to a high of 191.9 pounds per acre in the cropped pond Alpha in 1960. Differences in standing crops of perch were due in part to differences in pond fertilities, differences in pond treatments, and differences in size and/or age compositions of the populations. Fertilities of the three ponds in Unit 2 were believed to be quite similar, but all were clearly less fertile than the single pond Alpha. The degree of differences is indicated by the fact that the cropped pond Alpha had a larger standing crop in 1960 than did pond Theta in 1963 when it received quite large additions of stock.

The differences in standing crops in pond Alpha in 1959 and 1960 were not as large as indicated (Table 26) because 21.5 pounds were cropped from Alpha just prior to the October draining census in 1959, and this poundage is included under the heading "pounds removed." Without this October removal the standing crop in 1959 would have been approximately 144 pounds rather than 123.4. However, the "pounds gained" would have remained the same at 183.7 in 1959, regardless of how the standing crop was computed, which illustrates the usefulness of the pounds gained statistic.

Remaining differences in standing crops and in pounds gained or lost in pond Alpha in the two periods have been attributed to differences in schedules of cropping and in population composition. In 1959 cropping was poorly distributed over the growing season with a total of only 32.5 pounds removed by late July. Since average length increment of the dominant yearlings was only about 0.5 inch from May through September, 1959, and since coefficients of condition steadily declined from 4.25 to 3.78 during the same period, the removal apparently was too little to permit increased growth by survivors. In 1960 we wanted to determine if more intensive cropping of pond Alpha earlier in the season might have a more measurable effect on the survivors, and tend to increase total production. In 1960 24.5 pounds were removed in April, 22 in May, and a total of 77.2 pounds, or about 88 percent of the total season's cropping had been accomplished by July 20. Table 26 shows a marked increase in production during the second and shorter of the two periods. From an original stock of 19.4 pounds the first population showed a pounds gained figure of 183.7 pounds in two seasons, whereas the second population, with a much larger original stock (125 pounds), showed 155.2 pounds gained in only one growing season. The actual mechanisms were a greater production and/or survival of young, and increased growth by survivors of the original stock.

While the accelerated cropping surely increased production in 1960, there were also important differences in popu-

Table 26.—Pounds of yellow perch per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in the single pond Alpha for periods of 1 and 2 years, and in ponds Zeta, Theta, and Iota (Unit 2), for periods of 1, 2, and 3 years. All censuses were by pond drainage in the fall.

Unit	*Pond*	*Treatment*	*Year of Census*	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
—	Alpha	Cropped	1959	2	19.4	123.4	0.0	79.7	+183.7
—	Alpha	Cropped	1960	1	125.0	191.9	0.0	88.3	+155.2
2	Iota	Control	1961	1	51.8	94.7	0.0	11.9[a]	+ 54.8
2	Iota	Control	1963	2	47.7	100.3	0.0	62.1[b]	+114.7
2	Theta	Add-stock	1963	3	54.3	183.7	149.9	39.5[c]	+ 19.0
2	Zeta	Cropped	1963	3	53.3	51.3	0.0	222.8[d]	+220.8

[a] Removed primarily for study purposes.
[b] Of this total 29.9 pounds were removed in 1962 and 32.2 in 1963, primarily to reduce the extremely abundant 1962 brood and to strengthen the weak brood of the same year in pond Theta.
[c] Of this total 7.1 pounds were removed in 1961, 29.6 in 1962, and 2.8 in 1963, primarily for study purposes.
[d] Of this total 60.1 pounds were removed in 1961, 103.8 in 1962, and 58.9 in 1963.

Table 27.—Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of yellow perch in the single pond Alpha, and in ponds Zeta, Theta, and Iota (Unit 2), in years indicated. Age groups are shown in italic Roman numerals.

Pond, Year of Census, Treatment[a]	Total Number Censused in Each Age Group					Percent of Total Number Censused in Each Age Group					Percent of Total Weight Censused in Each Age Group					Total, All Age Groups	
																Number	Pounds
	0	*I*	*II*			*0*	*I*	*II*			*0*	*I*	*II*				
A 1959 0	464	1,531	2			23.2	76.7	tr			12.7	86.6	0.7			1,997	123.4
	0	*I & II*				*0*	*I & II*				*0*	*I & II*					
A 1960 0	14,288	764				94.9	5.1				50.1	49.9				15,052	191.9
	0	*I*	*II & III*			*0*	*I*	*II & III*			*0*	*I*	*II & III*				
I 1961 0	0	2,210	66			0.0	97.1	2.9			0.0	89.8	10.2			2,276	94.7
	0	*I*	*II*	*III*	*IV*	*0*	*I*	*II*	*III*	*IV*	*0*	*I*	*II*	*III*	*IV*		
I 1963 0	0	3,079	0	372	19	0.0	88.7	0.0	10.7	0.6	0.0	59.2	0.0	30.7	10.1	3,470	100.3
T 1963 +	141	2,861	0	998	14	3.5	71.3	0.0	24.9	0.3	2.0	64.0	0.0	30.0	4.0	4,014	183.7
Z 1963 —	752	230	0	30	3	74.1	22.7	0.0	3.0	0.3	40.8	42.2	0.0	13.7	3.3	1,015	51.3

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[a] Ponds are designated as: A = Alpha, Z = Zeta, T = Theta, and I = Iota. Pond treatments are designated as: O = none, + = stock added, and — (minus) = cropped.

lation compositions. The first relates to the increased abundance of breeding stock in 1960, which resulted in an increased production of young-of-the-year. The only mature females present in 1959 were survivors from the original stock of four, since females of the 1958 brood would not have matured by 1959. In 1960, however, the 1958 brood was in its third year, and is known to have spawned. Weight of Age O perch in the final censuses increased from 15.7 pounds in 1959 to 96.2 pounds in 1960.

A second important difference in composition of the two populations in pond Alpha was in their size distribution. In the 1959 census, in excess of 99 percent of the population, both by weight and by numbers, was contained within a length range of only 3.3 inches (from 4.1 to 7.4). Concentration into such a small size range undoubtedly intensified competition for food and greatly restricted predation of the smaller by the larger perch. In contrast, when censused in 1960 the population was quite normally distributed over a range of 7.2 inches (from 2.5 to 9.7), which could have permitted substantial cannibalism and a more efficient utilization of total food resources. Age O fish grew more slowly in 1960 than in 1959 because of their much greater abundance, but both growth and condition of fish older than Age O improved in 1960.

When this pond was devoted to smallmouth bass an initial stock of 16.16 pounds of small breeders produced a standing crop of 64.7 pounds after one and one-half growing seasons. The standing crop of perch in 1959 approximately doubled, and the 1960 crop approximately tripled this previous production of smallmouths.

Standing crops of perch in Unit 2 ponds ranged from 51.3 pounds in cropped Zeta in 1963 to 183.7 in the add-stock pond Theta in the same year (Table 26). The control pond Iota was drained and censused at the end of only one growing season (October, 1961), and was restocked and censused again after two additional growing seasons (October, 1963). Standing crops were similar at 94.7 and 100.3 pounds in 1961 and 1963 respectively. One might therefore conclude that the carrying capacity of this pond for perch was approximately 100 pounds per acre. It seems likely, however, that production may have been inhibited, and standing crops depressed by poor production of young in both census years. For reasons unknown no young were produced, or none survived, in 1961, a strong year-class was produced in 1962, and there was another complete failure in 1963. Thus neither the 1961 nor 1963 census contained young-of-the-year. The presence of young would have increased total poundages and would have provided food for older, cannibalistic individuals. The carrying capacity of this pond (Iota) may therefore have exceeded the poundages obtained from the two censuses. It should be noted that the maximum standing crop of largemouth bass in this pond had been 71.7 pounds when it was used as an add-stock pond in 1960.

As might be expected, pounds gained were lowest and standing crop highest in the add-stock pond, and pounds gained were highest and standing crop lowest in the cropped pond. The differentials reflect an increased productivity associated with cropping. For example, with the addition of stock the pounds gained figure in pond Theta amounted to only 19 pounds, compared with 220.8 pounds gained where cropping was heavy. Here pounds gained was almost equal to the total of pounds removed, indicating a complete turnover of the population.

Effects of Cropping on Fish Production

The influences of cropping on perch populations were perhaps less obscured by environmental differences than in experiments with either of the basses. We

Table 28. — Growth of yellow perch in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on yellow perch in several other waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
....	Alpha	1959	Cropped	4.4 (100)	5.7 (100)	..	..
....	Alpha	1960	Cropped	2.7 (100)	..	..	..
Unit 2	Iota	1961	Control	..	4.8 (300)	..	..
Unit 2	Iota	1963	Control	..	3.8 (200)	..	6.0 (155)
Unit 2	Theta	1963	Add-stock	3.9 (15) [a]	4.7 (230) [b]	..	5.1 (202) [c]
Unit 2	Zeta	1963	Cropped	4.3 (200)	6.2 (230)	..	7.9 (29)
Other Waters		*Author*					
Lake Chautauqua, Ill.		Starrett and Fritz (1965)		..	7.1	8.3	9.7
Lake Erie		Jobes (1952)		3.6	6.6	8.4	9.4
Red Haw Lake, Iowa		Lewis (1950)		3.7	7.2	10.3	..
East Lake, Iowa		Lewis (1950)		3.4	5.7	7.1	7.6

[a] Determined from fish spawned in the pond.

[b] Determined from those fish spawned in the pond or transferred as fry from pond Iota in June, 1962.

[c] Determined from survivors of the original stock.

have already noted the increased production in pond Alpha in 1960, over that of the 1958–1959 period, due at least in part to accelerated cropping in the latter year. The same was equally evident in Unit 2 ponds where the figures for both pounds gained and growth (length of the fish) were greater in the cropped than in either companion population (Tables 26 and 28). Table 27 shows that the largest standing crop produced by perch was that containing the greatest abundance of young-of-the-year. Table 27 also shows that the strength of the Age O year-class was related to the abundance of older perch, particularly those of Age I. Thus where Age I perch were abundant in the final census, Age O perch were scarce or absent. We suspect that the absence of Age O perch was due in large part to predation by Age I perch when Age O perch were very young. We believe that the cropping of Age I perch increased the survival of young.

Growth and Condition

In the marking experiments in pond Alpha in 1960 we gained useful information on rates of seasonal growth. Table 29 includes figures indicating the percent by which each monthly lot increased its average length between time of marking and time of the October census. The greatest average length increment was 17.6 percent made by fish marked in May, and those marked in both May and June made larger increments than those marked in April. After May the rates declined quite regularly to a low of 4.9 percent for perch marked in mid-September.

The differences in growths made by perch marked in May and June and those marked in April are believed to be sex related. Samples for all three months were collected by wire traps, and length-frequency data indicated the samples to be almost equally divided between Age I and Age II individuals. More than 90 percent of the April sample was com-

Table 29. — Averages and ranges in total lengths of yellow perch marked in pond Alpha in spring and summer months indicated in 1960, and recovered in the fall draining census, with percents of mortality and length increments for each monthly lot.

Marked (During periods indicated, in 1960)				*Recovered (Nov. 7-9, 1960)*				
Date	Number	Range in Length, Inches	Average Length, Inches	Number	Range in Length, Inches	Average Length, Inches	*Percent Mortality*	*Percent Length Increment*
April 5–6	60	4.2–6.1	5.03	43	5.2–6.8	5.90	28.3	14.7
May 10–13	60	4.2–6.3	5.18	49	5.4–8.1	6.29	18.3	17.6
June 1–2	60	4.6–6.9	5.44	55	5.5–8.5	6.43	8.3	15.4
July 6–8	60	5.2–6.9	5.90	46	5.4–8.1	6.40	23.3	8.5
Aug. 29	52	5.5–8.2	6.83	38	6.0–9.7	7.19	26.9	5.0
Sept. 14–15	40	5.5–8.1	6.85	35	5.7–8.7	7.20	12.5	4.9

posed of ripe, freely milting males, and the few females caught at that time were retained for stocking a different pond. Fish marked and released in April are therefore known to have been all males. Spawning occurred in April, and fish marked in May and June were not sexed, but were believed to have had a more normal sex ratio. We therefore believe that the smaller increment made by the exclusively male sample marked in April reflects a poorer growth made by this sex. These data seem to be somewhat at variance with those of Herman *et al.* (1959) who showed that among Age I and Age II perch from Green Bay and Lake Mendota the males were of similar or slightly larger average size than females, but that the females were larger by Age III and thereafter.

Growth data presented for comparison with data from other waters (Table 28) are restricted to fish recovered in the draining censuses, and for which ages were known (not calculated). Data presented in the growth curves (Fig. 6 and 7) are based on samples collected on the dates indicated. Some such samples were collected on a single day and others represent a composite of small collections over periods which rarely exceeded 10 days. Perch samples were collected by wire traps, hook-and-line, and by boat shocker. Ages of fish were known by presence or absence of marks, or by distinct separations in size. First-year growths compared favorably with those from other waters (Table 28), except when the age class was unusually large, as in pond Alpha in 1960 in the presence of abundant, protective vegetation. Good first-year growth was probably related to heavy predation by older perch. Growth by perch older than Age O in our single-species populations was very poor, and poorer than for perch in most other waters with which they were compared. For example, growth increments of the 1960 year-class over a 2-year period (Ages II and III) in our control and add-stock ponds (Unit 2) were only 1.24 and 0.69 inches respectively. Concurrent growth in our cropped pond was higher, but still only 2.26 inches.

The influences of cropping and additions of stock are apparent in Fig. 6 and 7 which present growth and condition curves for the 1960 and 1962 year-classes throughout their existence in the populations. For the dominant 1960 year-class (Fig. 6) growth was fastest in the cropped pond, slowest in the add-stock pond, and intermediate in the con-

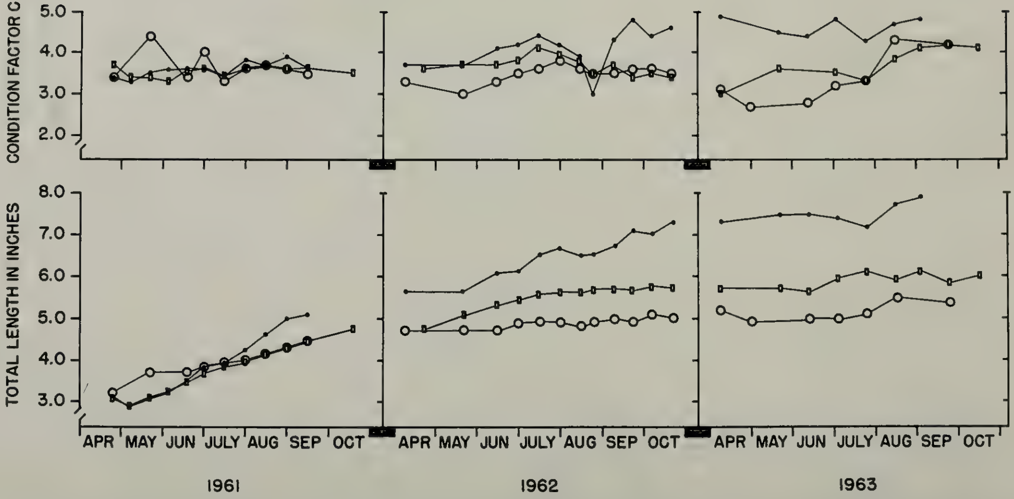

Fig. 6.—Growth and condition (C) of yellow perch of the 1960 year-class in the control pond Iota (rectangles), add-stock pond Theta (circles), and cropped pond Zeta (dots) during the 1961, 1962, and 1963 growing seasons.

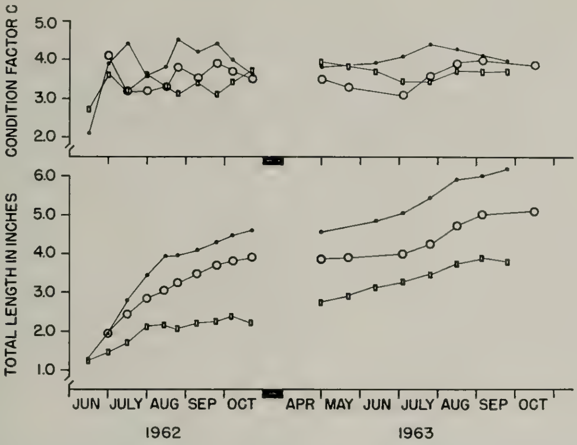

Fig. 7.—Growth and condition (C) of yellow perch of the 1962 year-class in the control pond Iota (rectangles), add-stock pond Theta (circles), and cropped pond Zeta (dots) during the 1962 and 1963 growing seasons.

trol pond, and the relationship of condition to growth was generally normal and consistent, with highest condition associated with fastest growth.

The next most dominant year-class through 1962 and 1963, both by weights and numbers, was that spawned in 1962. Fig. 7 shows that both condition and growth in the cropped population were again high, but that both growth and condition in the add-stock pond quite consistently exceeded that of the control pond. The explanation lies in the comparative abundance of the age class in the two populations. Spawning success was extremely poor in pond Theta in 1962, but exceptionally heavy in the control pond Iota. In June 1962, 2,380 Age O perch were transferred from Iota to Theta. The abundance in Iota was still such that an additional 14,664 fish of this age were thinned from Iota, mostly in 1962. By time of final census in October, 1963, this 1962 brood still numbered 3,079 in Iota, as compared to 2,861 in pond Theta, and only 230 in the cropped pond Zeta. In pond Theta the lesser number of this age class grew faster and maintained better condition, even though the number and total weight of older perch was much larger in this add-stock (Theta) than in the control (Iota) population. Thus, rate of growth was more dependent upon abundance of the year-class (intra-year-class, or size competition) than upon total standing crop, or total population pressure. This indicates a diversity of food habits by size, and that a group of one size can make fast growth in the presence of an abundance of larger, more slowly growing fish, the latter apparently offering little competition for food or other essentials of the environment.

Table 30 presents a comparison of the growth and condition of the various components of the Age I and Age III perch in the final census of pond Theta in relation to their origin or date of transfer. For both age groups final average lengths and weights were greater for perch of the original stock than for those perch moved to the add-stock pond in

Table 30. — Averages of total lengths, weights, and coefficients of condition of various components of Age I and Age III yellow perch in the final census of the add-stock pond Theta, 1963, in relation to their origin or date of transfer.

	Length, Inches	Weight, Pounds	Coefficient of Condition
Age I			
Original Stock	4.67	0.037	3.63
Transferred in 1962	4.54	0.034	3.63
Transferred in 1963	5.75	0.073	3.84
Age III			
Original Stock	5.07	0.046	3.53
Transferred in 1961	4.89	0.040	3.42
Transferred in 1962	6.94	0.130	3.89
Transferred in 1963	7.73	0.200	4.33

the first year in which each was transferred (1962 for Age I perch, 1961 for Age III perch). We know that in all cases fish transferred from the cropped to the add-stock population were of larger average size at time of transfer than perch of the same age among the original stock in the add-stock population. Since transferred fish received no harsher treatment than fish of the original stock which were sampled, weighed, marked, and returned to the add-stock population, the retardation of growth would have been due more to stresses encountered in the new environment than to handling. Progressively greater average sizes of perch transferred at later dates reflects the growth advantage obtained before transfer from the cropped population. Comparative data on condition are generally consistent, with fish transferred latest having the highest coefficients of condition.

Mortalities

In 1960 we were able to compute total mortality of perch older than Age O in pond Alpha. From an original stock of 2,017 "older" fish, 1,089 were removed by cropping and 764 were recovered in the final census, leaving an unaccounted for loss of 164, or about 8.1 percent of the original stock.

In 1960 we also attempted to obtain rates of seasonal mortalities, along with rates of seasonal growth. From April through September a number of perch of Ages I and II were caught and released with a distinctive mark for each month. As in earlier, similar experiments with smallmouth and largemouth bass, the data provided little useful information on rates of seasonal mortality and emphasized the difficulties of such an experiment. For example, lowest mortalities were among fish marked in June, and mortalities for fish marked in July and August were much higher than for those marked in June and little different from mortalities of those marked in April (Table 29).

From marks given to various year-classes, and to fish transferred to pond Theta, we have information on mortalities of many components of the populations from ponds Zeta, Theta, and Iota. Our most complete information is from pond Theta, which received additions of stock. Among the 141 Age O fish recovered in the final census, 126 were survivors of the 408 transferred from pond Zeta in July and August, 1963 (69.1 percent mortality) and only 15 were survivors from the 1963 brood spawned in this pond. These returns indicate a rather heavy predation of young by older perch.

Recoveries in the draining censuses and computed mortalities for various categories of perch are presented in Table 31 for the control pond Iota, in Table 32 for the cropped pond Zeta, and in Table 33 for the add-stock pond Theta. Mortalities were generally quite irregular and not clearly density-related, *i.e.*, not notably or consistently higher in the add-stock population than in the cropped or control populations. This indicates that density probably was not a critical factor among our populations. However, mortalities were higher among fish transferred to a new population than among members of the original stock already resident in that population. For example, for three groups of perch, all of the 1960 brood, mortalities by October 1963 were 96.1 percent among 462 perch transferred in 1962 and 85.1 percent among 1,309 transferred in 1961, while mortality of original stock over the 3-year period was only 74.4 percent (Table 33). While fish densities did not appear to be critically high, transferred fish encountered stress in the new environment which increased their mortality. As mentioned before, the act of marking and transfer was not in itself cause for greater mortality because untransferred fish were also marked and handled.

Table 31. — Mortalities of various categories of yellow perch in the 1961 and 1963 October draining censuses of the control pond Iota, approximately 11 months and 24 months after stocking.

Year Class or Classes	*Recovery in Oct., 1961 of Fish Stocked in Nov., 1960*	*Recovery in Oct., 1963 of Fish Stocked in Oct., 1961*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	2,210 of 3,771	..	140	39.1
1958–59	66 of 225	..	70	57.4
1960	..	372 of 1,000	30	61.6
1958–59	..	19 of 65	0	70.8

Table 32. — Mortalities of original stock of yellow perch in the October, 1963 draining census of the cropped pond Zeta.

Year Class or Classes	*Recovery of Fish Stocked in Nov., 1960*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	30 of 3,771	2,877 [a]	96.6
1958–59	3 of 225	216 [b]	33.3

[a] Removed 1,704 in 1961, 1,088 in 1962, and 85 in 1963.
[b] Removed 213 in 1961, 0 in 1962, and 3 in 1963.

Table 33. — Mortalities of various categories of yellow perch in the October, 1963 draining census of the add-stock pond Theta.

Year Class or Classes	*Origin, or Number Orginally Stocked in Nov., 1960*	*Recovery in Oct., 1963 of Original Stock, or of Fish Marked and Transferred to Theta in Year Indicated*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1963	Transf. from Zeta	126 of 408 (1963)	0	69.1
1962	"	299 of 385 (1962)	0	22.3
1960	"	58 of 83 (1963)	0	30.1
1960	"	18 of 462 (1962)	4	96.1
1960	"	194 of 1,309 (1961)	8	85.1
1960	3,771	728 of 3,771 (O.S.) [a]	926 [b]	74.4
1958–59	Transf. from Zeta	3 of 3 (1963)	0	0.0
1958–59	225	10 of 225 (O.S.) [a]	0	95.6
1958–59	Transf. from Zeta	1 of 155 (1961)	50	99.0

[a] Indicates original stocking of November, 1960.
[b] Total of 926 includes 62 cropped in 1961, 855 in April, 1962, and 9 in May, 1963.

Spawning Success

Variations in spawning success and in year-class strengths were large and of particular interest in the perch populations. Adequate breeding stock was present in the form of Age III perch in all ponds in 1961, but all three populations failed to either spawn or produce a surviving year-class in this first spawning season in the Unit 2 ponds. In the control pond Iota a strong year-class was produced in 1962, having 3,079 survivors in the fall of 1963, and this was followed by an extremely light year-class in 1963, of which none survived to the end of that year.

Theta, the add-stock pond, produced no surviving young in 1961, and there was extremely light reproduction (or survival) in both 1962 and 1963.

Zeta, the cropped pond, after its 1961 failure, produced a large year-class in 1962. However, this class was drastically thinned by mortality of unknown origin. Over a 2-week period in early June, 1962, the 1-to 2-inch fingerlings could be seen at the surface periodically immobile and "belly-up" for a few seconds, from which they would suddenly recover as if under some sudden stimulation and swim rapidly away, only to repeat the process a few minutes later. While no mortalities were observed at the time, subsequent sampling revealed a greatly reduced population of the Age O fish. Only 230 survived until October, 1963. Fish older than Age O apparently were unaffected. The heavy 1962 spawn was followed by a weak brood in 1963, of which only 752 were recovered in October of that year.

A normal spawn was anticipated in 1961 because both ripe and spent females were observed, and developing eggs were found on wire traps. When the failures became apparent we speculated that the cause may have been due to the absence of submerged vegetation in ponds Zeta, Theta, and Iota, and that successful spawning in Alpha may have been facilitated by an abundance of Chara. Starrett & Fritz (1965) attributed poor spawning success of yellow perch in Lake Chatauqua to the lack of submerged vegetation. Though moderately thick growths of pondweeds (*Potamogeton* spp.) developed in the summer months in our ponds, none were present during the spawning period. As a spawning aid in 1962 and 1963 multibranched tree limbs were placed in the ponds. Eggs were deposited upon the limbs in both years, and eggs transferred from the limbs to the laboratory made normal development. Reproduction was heavy in Zeta and Iota in 1962, and light in Zeta and Theta in 1963, but no young were recovered from Iota in 1963. Obviously, some additional factor was limiting.

Our data indicated that high pH was not a limiting factor in the reproduction of perch, and that water quality was otherwise satisfactory. We suspect that under conditions of normal water quality, failures of reproduction are due less to failure of the adults to produce normal eggs and young than to a failure of the young to survive. Fluctuations in year-class strength are common to perch populations (Herman *et al.* 1959), as to most fish species. In the present instance we believe the most probable cause was predation on eggs or young. Failures occurred when either weight or numbers of companion perch (principally Age I) were large, and successes occurred when they were small (Table 27). Though the populations were not large by normal standards, they occurred in the absence of protective cover for young. Abundant spawns in pond Alpha could have been facilitated by the protective cover provided by the beds of Chara, but no such protection existed in the ponds in Unit 2. Predation of eggs or larvae by large populations of crayfish and tadpoles may have augmented that by perch. Both forms were of unusual abundance in 1962 and 1963 because of the absence of bass or other large predators.

Related Environmental Factors

Although quantitative data are limited, some observations can be made of such related ecological factors as abundance of associated plants and animals, and of the physical and chemical characteristics of the pond waters. Of particular note were the unusual abundances of tadpoles and crayfish, presumably because of the absence of bass or other more efficient predators. Table 34 presents weights of these forms, together with weights of perch collected during the final censuses. As indicated in the table footnote, poundages of crayfish were conservative, because many failed to be flushed from the pond with the water and were not available for weighing. Poundages presented, however, are believed quite representative of differences in weights which occurred.

Tadpoles were primarily those of the bullfrog, *Rana catesbeiana*, crayfish were identified as *Arconectes virilis*. There are several noteworthy associations in Table 34.

1. The largest poundages of perch were associated with the smallest poundages of crayfish, and vice versa, indicating some degree of control of crayfish by perch.
2. Tadpoles were abundant when crayfish were scarce, and vice versa, indicating some degree of control of tadpoles by crayfish.
3. At the time of the three 1963 drainages, weeds (principally *Anacharis* sp.) covered an estimated 90 percent of the bottom of pond Theta, which had the fewest crayfish, while the bottom was almost completely bare of weeds in pond Zeta with its comparatively great weight (231.2 pounds) of crayfish. Neither weeds nor crayfish were abundant at the two drainages of pond Iota. Actually, weeds in all three ponds had been quite drastically thinned by treatments with endothal in June, 1963, but the weeds had again become abundant where the crayfish were less abundant and had become increasingly scarce where the crayfish were most abundant.

Nymphs of the large burrowing mayfly, *Hexagenia limbata*, were abundant in ponds Iota and Zeta, but were absent from pond Theta at the time of drainage in October, 1963. At the time, the bottom of pond Theta contained thousands of small "craters" from 1 to 3 inches in diameter, and from 1 to 1½ inches deep, often with subsurface cavities larger than the openings. Since these craters were not present in the companion ponds having abundant burrowers, it suggests that the larger population of perch in Theta may have eliminated the mayflies by burrowing or sucking them out of the mud. Concurrently, however, scuds, phantom larvae, smaller mayflies, dragonflies, and assorted other

Table 34. — Standing crops of yellow perch, crayfish, and tadpoles, and relative abundances of rooted, submerged aquatic plants in ponds Zeta, Theta, and Iota at times of fall draining censuses.

Pond and Year	*Standing Crop, Pounds Per Acre*			*Relative Abundances of Aquatic Plants*
	Yellow Perch	Crayfish[a]	Tadpole	
Iota, 1961	94.7	27.7	297.4	Medium
Iota, 1963	100.3	84.3	312.1	Medium
Theta, 1963	183.7	34.1	247.5	High
Zeta, 1963	51.3	231.2	84.3	Low

[a] Weights of crayfish are conservative because some did not flush out of pond.

invertebrates were of the same general abundance in Theta as in the companion ponds, suggesting no inordinate predation pressure on these forms.

Throughout most of each of the three growing seasons weekly observations were made of the surface pH, Secchi disc transparency, and the temperature profile of each pond. Because of differences in treatments of the populations, no interpretations can be made of the influence of these factors upon fish production. However, the data warrant the following observations.

Of the three years, thermal stratification was greatest, and transparency lowest in all ponds in 1963. The decrease in average transparency was negligible in the add-stock pond, but quite marked in the companion ponds, particularly the cropped pond Zeta (from 72 inches in 1961 to 20 inches in 1963). One therefore suspects that decrease in transparency was related to increase in the crayfish population, which was notably high in pond Zeta. Increase in thermal stratification was in turn probably related to decrease in transparency of the pond water.

Differences in pH were not believed to have had any important influence on fish production. Generally lower pH's in 1963 were probably related to the reduction of weeds by chemical treatment in all ponds in June, 1963. A lesser average pH in pond Zeta was probably related to the influence of crayfish in reducing vegetation in that pond.

Review of Perch Data, and Comparison with Largemouth and Smallmouth Data

Perch were maintained in ponds previously occupied by either smallmouth or largemouth bass. In Unit 2 ponds the maximum standing crop obtained from a control population of largemouths was about 50 pounds per acre, while that for a population of perch receiving the same treatment was about 100 pounds. The largest standing crop obtained from an add-stock population of largemouths in this unit was about 72 pounds, while that from the add-stock population of perch was about 184 pounds.

We have already noted that in pond Alpha the standing crop of perch in 1959 more than doubled, and that of 1960 approximately tripled, the standing crop of smallmouths earlier produced in this pond. We believe, however, that the differences in efficiencies in food utilization or conversion were less than indicated. Smallmouth bass probably did not attain their potential maximum in pond Alpha because of the relative immaturity of the pond when occupied by smallmouths, and because the population had developed over only one and one-half growing seasons and contained only two year-classes when censused.

Perch are believed to be more dependent upon an invertebrate diet than either of the basses, and their greater efficiency is probably related to their lower trophic level. However, in our data the yellow perch of intermediate size and age appeared to be less efficient in utilizing invertebrate foods than were smallmouth bass of the same category. The largest standing crops of perch were those having the largest numbers of young-of-the-year, and where young were scarce, older fish seemed incapable of taking up the slack or of making efficient use of the food that would have been eaten by the young-of-the-year. On the other hand, our largest standing crops of smallmouth bass were those dominated by fish older than Age O, and production in these populations seemed very little inhibited by an absence or scarcity of young-of-the-year smallmouths. It may therefore be that in the absence of vertebrate food the smallmouth is a more efficient insectivore than the yellow perch.

Data from the add-stock population in Unit 2 indicate that the perch may be less versatile or adaptable in its food habits, and that there may be relatively less competition for food between different sizes and ages of perch than between different sizes and ages of smallmouths. We have seen, for example, that in the 1963 census of pond Theta, 2,861 perch of the 1962 brood had an average length only about 0.4 inches less than that of 728 perch of the 1960 brood. While the younger perch had grown almost 5 inches in 2 years, the older perch had grown less than 1 inch over the same period. Thus the younger, more abundant, faster-growing perch obviously utilized foods not taken by the older fish, which permitted them to literally grow into the size range of the older perch.

BLUEGILLS

Bluegills were studied in ponds Kappa, Lambda, and Rho (Unit 3) over a 3-year period, 1961–1963. This unit of ponds had been constructed in 1957, and for the period 1958–1960 was stocked with white crappies. Following the final census of crappies in October, 1960, each pond was stocked with 4,080 Age O bluegills from the state hatchery at Spring Grove, Illinois. Over the period May 11–June 23, 1961, each pond received an additional stock of 104 adult bluegills obtained by boat shocker from Fox Lake, Lake County, Illinois. The combined total weights of young and adults stocked in each pond were similar, ranging from 34 to 38.3 pounds (Table 35).

Standing Crop Data

Table 35 presents standing crop data for four bluegill populations together with such pertinent supplementary data as pounds of original stock, pounds added to or removed from the populations during the course of the experiments, and the net gain or loss in pounds of fish flesh by the termination of the experiments. Table 36 presents numbers in each size or age group and percentages of total numbers and weights of each group recovered in each

Table 35. — Pounds of bluegills per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Kappa, Lambda, and Rho, for periods of 1, 2, and 3 years. All censuses were by pond drainage in the fall.

Unit	*Pond*	*Treatment*	*Year of Census*	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
3	Rho	Control	1961	1	34.0	127.1	0.0	3.7	+ 96.8
3	Rho	Control	1963	2	38.5	99.8	0.0	17.5	+ 78.8
3	Kappa	Add-stock	1963	3	37.0	173.3	60.8	17.9	+ 93.4
3	Lambda	Cropped	1963	3	38.3	101.0	0.0	141.3	+204.0

Table 36.— Numbers in each age group and percents of total numbers and weights of each age group in censused populations of bluegills in ponds Kappa, Lambda, and Rho (Unit 3) in years indicated.

Pond, Year of Census, Treatment[a]	Total Number Censused in Each Age Group					Percent of Total Number Censused in Each Age Group					Percent of Total Weight Censused in Each Age Group					Total, All Age Groups	
	0	I	II	III	IV	0	I	II	III	IV	0	I	II	III	IV	Number	Pounds
R 1961 0	75,424	2,229	45	0	0	97.1	2.9	*	0.0	0.0	41.8	49.1	9.0	0.0	0.0	77,698	127.1
R 1963 0	67,453	2	346	468	31	98.8	*	0.5	0.6	*	12.1	*	24.9	53.0	10.0	68,300	99.8
K 1963 +	98,778	0	1,973	627	53	97.4	0.0	1.9	0.6	*	17.3	0.0	48.8	26.7	7.3	101,431	173.3
L 1963 —	8,644	0	1,438	10	0	85.7	0.0	14.2	*	0.0	28.5	0.0	69.2	2.2	0.0	10,092	101.0

[a] Ponds are designated as: K = Kappa, L = Lambda, and R = Rho. Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.
* Less than 0.01 percent.

draining census. Small poundages were removed from both control and add-stock ponds in all years, primarily for study purposes. The total of 141.3 pounds shown removed (Table 35) from the cropped pond Lambda is a minimum figure. Of this total 16.9 pounds of mixed Age I and adults were cropped in 1961, of which 15.5 pounds were transferred to pond Kappa. Known cropping from Lambda in 1962 consisted of mixed Age I (37.4 pounds), Age II (17.3 pounds), and original adults (17.5 pounds) for a total of 72.2 pounds. However, a significant part of this cropping was achieved on May 31, 1962 by spraying rotenone over a 30- to 40-foot width of approximately one-half of the shoreline. We hoped to achieve an early-season kill of a large proportion of the abundant Age I fish. A 3-day pickup of all visible dead included 4,616 bluegills (12 adults, 115 Age II, 4,489 Age I) weighing 15.9 pounds, which are included in the total of pounds removed (Table 35). Many fish (particularly Age I) were observed to sink to the bottom and be attacked by an abundant crayfish population, and were thus lost from the records. This unknown weight is believed to have been something less than that recovered and recorded from the treatment. Thus, the true pounds cropped, and pounds gained, were in excess of those totals listed in Table 35.

In 1963 a total of 52.1 pounds was cropped from pond Lambda including 10,954 young-of-the-year weighing 16.9 pounds, removed in August, and 719 Age II fish weighing 35.2 pounds, removed in June, July, and August. Of this total, 626 Age II fish weighing 30.7 pounds were transferred to pond Kappa.

Standing crops of bluegills in pounds per acre ranged from 99.8 in the control pond Rho in 1963 to 173.3 in the add-stock pond Kappa in the same year. As in our previous experiments, variations in production by the separate populations were influenced by differences in 1) treatments received, 2) population compositions, and 3) pond fertilities; however, the relative importance of each factor was difficult to assess. We may first note that standing crops (pounds) were highest where numbers of both Age O and older bluegills were largest (Table 36). There is evidence, however, that the add-stock pond had the additional advantages of greater fertility and a larger carrying capacity. It seems significant that even with the much larger standing crop in the add-stock pond, its pounds gained figure was also greater than in the control population (Table 35). Thus, pond Kappa made a substantial production of fish flesh in addition to that transferred from the cropped pond. This suggests that the additions to pond Kappa had not exceeded the pond's carrying capacity. Since the numbers of both small and large fishes contained in pond Rho appeared sufficient to utilize available food resources, we must suspect that the carrying capacity of pond Rho was much smaller than that of pond Kappa in 1963.

We have evidence that the carrying capacity of the control pond Rho declined quite substantially between 1961 and 1963. Table 35 shows that in this pond both final standing crop and pounds gained figures were substantially higher in 1961 than in 1963. We may note (Tables 35 and 36) that final population structures were comparable, having similar abundances of both small and large bluegills, that original stocks were similar, and that differences in pounds removed were not significant. We thus have evidence that the carrying capacity of pond Rho had been attained in its first growing season (1961), that a greater weight of fish was produced in the first than in either of the two following seasons, and that the productivity of this pond declined quite substantially between 1961 and 1963 in spite of moderate fertilization in 1962. It also seems significant that final standing crops of both crayfish and tadpoles were also higher in Rho in 1961 than in 1963. Pounds of crayfish in 1961 (173.2) were more than triple the amount of 1963 (55.6), and pounds of tadpoles in 1961 (113.9) more than doubled the standing crop (55.9) of 1963.

The final population in pond Rho in 1961 contained 75,424 young-of-the-year which comprised about 42 percent of the total weight of the standing crop. The 1963 census of Rho also contained abundant Age O fish (67,453), but these comprised only 12 percent of the total weight due to their smaller average size. This smaller size suggests that spawning in 1963 may have been later than in 1961, or that food for young was in shorter supply. With regard to date of spawning, our field notes indicate that spawning occurred in late June or early July in both years, with young of similar sizes first found in early July in both years. Our sampling provided no evidence of a second and larger spawn in late 1963. We believe that the young-of-the-year simply grew more slowly in 1963, in spite of their lesser abundance.

We have no comparative data on abundance of benthos or zooplankton in the two years. However, data on mean seasonal transparencies (Secchi disc) show that pond Rho maintained a richer bloom in 1963 than in 1961. Means of weekly readings from April through October were 19 inches in 1963 and 45 inches in 1961. Higher turbidity in 1963 than in 1961 was not caused by crayfish since the standing crop of crayfish in 1963 was only about one-third as great as that in 1961 when turbidities were lowest. These ponds received very little erosion silt, and never appeared muddy. Turbidities were due primarily to phytoplankton. The greater plankton turbidity in 1963 indicated a condition favorable to fish production in that year, a fact not borne out by the standing crop data. It seems apparent that the principal food utilized by the bluegills was not dependent upon phytoplankton abundance.

Mortalities were frequently high and quite variable, but were not believed to have had an important influence upon size of final standing crops. Dead fish were rarely seen, and no large or sudden "kills" were observed just prior to the censuses, or at any other time. The most probable effect of mortalities on the table data was in some instances an artificial depression of the pounds gained figure. For example, of the 626 Age II fish transferred to pond Kappa in 1963, only 102 were recovered in October of that year. A major portion of this mortality was probably due to handling, with a large proportion of the fish dying so soon as to have had a minimum impact upon the existing population. In our computations of pounds gained, however, the total weight of transferred fish was treated as though all had survived. Since this was a minus (subtracted) quantity in the calculations, the figure of pounds gained was artificially depressed, and production of fish flesh in the population was higher than indicated. This factor was probably more critical among bluegills than among other species studied because in our experience the bluegill was the most susceptible to injury or death due to marking and handling.

Effects of Cropping on Fish Production

Increased production gained by cropping was probably more clearly evident in the bluegill study than in those for other species. The key figures were those of pounds gained (Table 35). The figure of 204 pounds gained in pond Lambda was a minimum one due to unknown losses from the use of rotenone, yet it was more than twice that of either companion pond. It is significant that even with the cropping of 52.1 pounds from Lambda in 1963, its standing crop in October slightly exceeded that of the control pond Rho. It is also noteworthy that numbers in the final censuses were less than one-sixth as great in cropped Lambda as in the control population in pond Rho. A total of 10,954 young-of-the-year were cropped from Lambda in 1963, and the smaller number of 8,644 remaining in the final census represented 29 percent of the total weight of the population, while the much greater number of 67,453 Age O bluegills censused in pond Rho represented only 12 percent of the total weight censused in that pond. The fewer fish had grown much faster, indicating that total numbers are in themselves not an overriding factor. With no evidence of a greater inherent productivity in pond Lambda than in pond Rho, greater production of bluegill flesh in pond Lambda must have been stimulated by cropping.

Growth and Condition

Growths of bluegills in our single-species populations through their first 3 years of life were in most cases slower than for bluegills from normal, mixed populations in Illinois reservoirs with which they are compared (Table 37). Again, our growth data were from large samples of known-age fish as collected in the final censuses at the ends of the growing seasons. Failure of certain age classes in our cropped pond to show faster growth than in the companion ponds was due in some instances to differences in abundance. For example, the average length after three growing seasons was greater in the control pond Rho (4.9 inches) than in the cropped pond Lambda (4.3 inches) (Table 37), because the group in question (Age Group II, Table 36) numbered only 346 individuals in the final census in pond Rho, as compared to 1,438 in pond Lambda. At the same time, total lengths of 3-year-old fish were little different in the cropped and add-stock populations even though the add-stock pond contained the greater number of 3-year-old fish (1,973, as compared to 1,438) and total population pressure of fish older than Age O was much greater

Table 37. — Growth of bluegills in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on bluegills in other Illinois waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
Unit 4	Rho	1961	Control	1.13 (200)	3.57 (358)	..	..
Unit 4	Rho	1963	Control	0.75	2.78 (2)	4.90 (205)	5.62 (365)
Unit 4	Kappa	1963	Add-stock[a]	0.85 (100)	..	4.22 (253)	4.95 (141)
Unit 4	Lambda	1963	Cropped	1.82 (257)	..	4.30 (338)	6.76 (10)
Other Illinois Waters	*Author*						
Johnson Sauk Trail Lake	Rock (1966)			2.0	4.2	6.2	7.3
Ramsey Lake	Stinauer (1966)			2.7	3.7	5.0	5.5
Red Hills Lake	Price (1966)			2.6	4.0	5.4	6.0
Lake Chautauqua	Starrett & Fritz (1965)			1.8	4.8	6.2	7.1
Ridge Lake	Bennett (1954)			4.7	6.2	7.1	7.6

[a] Data presented for this population were taken from fish of the original stock or those spawned in the pond.

(2,653, as compared to 1,448) (Table 36). It seems clear that pond Kappa must have had a higher carrying capacity than pond Lambda, at least in 1963.

Additional growth data are contained in Fig. 8 and 9 which present growth and condition curves for the dominant year-classes — the 1960 year-class through 1961 and 1962 and the 1961 year-class through 1962 and 1963. Mean lengths and conditions were computed from the same samples. All samples were collected by seine, and were in most cases large, never averaging less than 43 per sampling period in any year, and often approximating 100. Ages were known by presence or absence of marks previously given. Effects of cropping on growth of the 1960 year-class in 1961 was little apparent until late season when the average size for this group was largest in the cropped pond, smallest in the add-stock pond, and intermediate in the control population (Fig. 8). The rather narrow differences remained consistent throughout 1962. The corresponding curves for rates of condition computed from the same samples conformed poorly with growth curves. While the growth curves climbed quite consistently and regularly upward, indicating small sampling variation, those for condition were quite erratic from period to period, most notably for bluegills in pond Rho between mid-June and Mid-July, 1962 (Fig. 8). Here our samples showed condition to drop from 7.9 in mid-June to 4.4 on July 1, and to improve sharply to a high of 8.3 on July 15. We suspect that these major variations may have been related to the spawning act. No surviving young could be found in ponds Kappa and Lambda in 1962, and the only survivors from the 1962 brood were two recovered from pond Rho in the census of 1963. Since the major loss in condition occurred precisely at the time spawning would have been expected, and occurred only in pond Rho, spawning may have been restricted to this population, as our other observations indicated. It is of further interest that lengths increased while rate of condition continued to decline in the pond Rho samples over the period from July 1 to mid-September, 1962. Since lengths

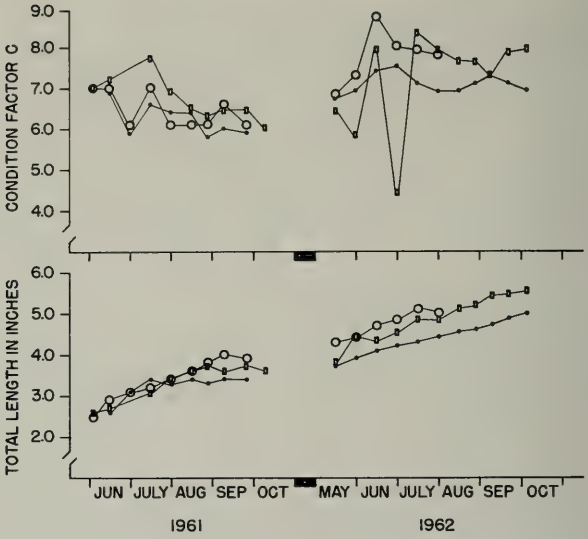

Fig. 8.—Growth and condition (C) of bluegills of the 1960 year-class in the control pond Rho (rectangles), add-stock pond Kappa (dots), and cropped pond Lambda (circles) during the 1961 and 1962 growing seasons.

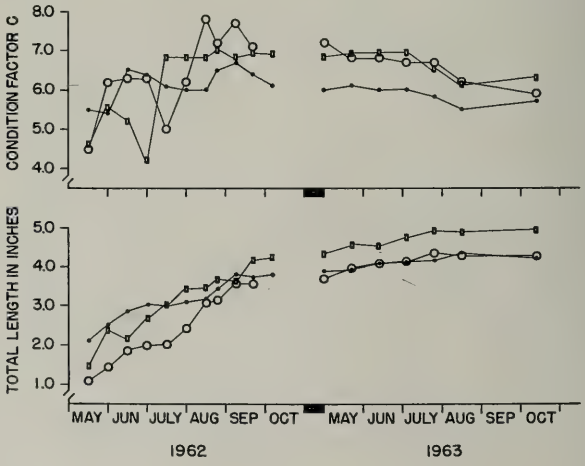

Fig. 9.—Growth and condition (C) of bluegills of the 1961 year-class in the control pond Rho (rectangles), add-stock pond Kappa (dots), and cropped pond Lambda (circles) during the 1962 and 1963 growing seasons.

showed a regular continuous trend, the source of variation was clearly in weights. A part of such variations could be attributed to differences in fullness of stomachs at times of measurement and a part to unusual sampling variation, but a principal source could have been a loss of weight by spawning females. It seems evident, however, that for a variety of possible reasons conditions can vary widely in fishes having similar patterns of linear growth, and that comparative rates of condition may be poor indicators of comparative rates of linear growth.

Fig. 9 presents similar data for the 1961 year-class in 1962 and 1963. Due to their greater numerical abundance, fish in the cropped pond grew the least in 1962, and their growth was little different from growth of those in the add-stock pond in 1963. However, growth curves climbed quite regularly and uniformly upward in all ponds before leveling off in August, 1963, indicating little sampling variability. Condition curves were again extremely irregular in 1962, but quite regular and comparatively stable throughout 1963. The difference in the two years may have been related to differences in feeding habits or in availabilities of food. When younger, in 1962, these fish may have been largely dependent upon zooplankton, with frequent, large fluctuations in condition corresponding to normal variations in the abundance of such food. When the fish were older and larger, in 1963, foods taken may have been more diversified, and of a more stable abundance, resulting in more stable rates of condition.

We have noted in Fig. 8 and 9 that comparative strengths of year-classes were reflected in rates of growth. We referred to comparative abundance of the same year-class in different ponds. It is of further interest to consider the influence of differing strengths of year-classes in the same pond. Dominant year-classes in our ponds derived from the original stock of 4,080 bluegills of the 1960 brood in each pond, and from the large broods spawned in all ponds in 1961. We should then remember that reproduction failed in all ponds in 1962. We may thus consider comparative growth of Age I fish in the presence or absence of the younger year-class. Based on our bimonthly sampling from April into October, Age I fish in all three ponds grew more in 1962 than 1961 (Fig. 8 and 9). The average length increment of the Age I fish in all three ponds in 1961 in the presence of abundant Age O fish was only 1.29 inches, compared to an average increment of 2.29 inches for Age I fish in 1962 in the absence of Age O fish. A large part of this difference was probably due to differences in degrees of competition between the two year-classes in the two years.

Mortalities

On the basis of returns of bluegills bearing distinctive fin clips given at the time of stocking or transfer we were able to compute mortalities for various age groups in the control pond Rho (Table 38) and the add-stock pond Kappa (Table 39). Mortalities for bluegills in the cropped pond Lambda could not be calculated because of the unknown loss occasioned by the use of rotenone in 1962.

Mortalities were frequently high, but quite erratic, and tended to be somewhat higher among those fish transferred to pond Kappa than for the original stock in either population. Highest mortality was among 626 Age II bluegills transferred to pond Kappa in June, July, and August, 1963. The recovery of only 102 in October represented a loss of 83.7 percent over a fraction of a growing season. These fish were handled in larger quantities than most groups sampled and/or transferred, and we believe that the longer period required for weighing, measuring, and marking these larger groups contributed to their higher

Table 38. — Mortalities of various categories of bluegills in the 1961 and 1963 October draining censuses of the control pond Rho, approximately 11 months and 24 months after stocking.

Year Class or Classes	*Recovery in Oct., 1961 of Fish Stocked in Oct., 1960, or May-June, 1961*	*Recovery in Oct., 1963 of Fish Restocked in Oct., 1961*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	2,229 of 4,080	. .	185	42.8
Unknown[a]	45 of 104	. .	0	56.7
1961	. .	346 of 10,756	6,343	92.2
1960	. .	468 of 700	32	29.9
Unknown[a]	. .	31 of 45	2	27.9

[a] Designates the adults in the original stock for which ages were unknown.

Table 39. — Mortalities of various categories of bluegills in the October, 1963 draining census of the add-stock pond Kappa.

Year Class or Classes	*Origin or Number Originally Stocked*	*Recovery in Oct., 1963 of Original Stock, or of Fish Marked and Transferred to Kappa in Year Indicated*	*Numbers Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1961	Transf. from Lambda	102 of 626 (1963)	2	83.7
1960	. .	36 of 87 (1962)	0	58.6
1960	. .	74 of 374 (1961)	0	80.3
Unknown[a]	. .	7 of 29 (1961)	0	75.9
Unknown[a]	. .	13 of 20 (1962)	0	35.0
Unknown[a]	104	33 of 104 (O.S.)[b]	1	68.0
1960	4,080	516 of 4,080 (O.S.)[b]	145	86.9

[a] Designates original stock of adults for which ages are unknown.
[b] Designates original stock.

mortality. Bluegills transferred in smaller groups in earlier years had smaller mortalities over longer periods of time. For example, for 374 bluegills transferred at Age I in 1961, and for 29 original adults transferred at the same time, mortalities by October, 1963 were 80.3 percent and 75.9 percent respectively. Mortalities among the control population were generally lower, but tended to be highest among the smallest fishes. For 10,756 Age O bluegills restocked following the 1961 census the mortality by October, 1963 was 92.2 percent. For 700 Age I bluegills and 45 of the original breeding stock restocked at the same time, mortalities by October, 1963 were only 29.9 percent and 27.9 percent respectively.

In 1961 we attempted to measure rates of seasonal mortality from April through September in pond Rho. In samples in each of these months approximately 100 Age I fish were captured and released with distinctive fin clips for each month, and returns of each mark were counted in the final census. As shown in Table 40, only 52 of 100 marked in June were recovered in October, but recoveries for fish marked in other months were grouped within a range of only about 75–78 percent. Differences in mortalities of bluegills marked in April and September were less than 2 percent. The similarities in the returns may indicate that there was a rather uniform loss due to handling and marking and that mortalities due to

Table 40. — Numbers of bluegills marked by a distinctive fin clip and released in each month of the growing season in pond Rho in 1961, numbers recovered in the draining census of October, 1961, and percents of mortality.

Month of Marking	*Fin Clipped*[a]	*Number Released*	*Number Recovered*	*Percent Mortality*
April	R. P.	99	74	25.3
May	L. P.	99	77	22.2
June	S. D.	100	52	48.0
July	H. D.	102	80	21.6
Aug.	Anal	101	77	23.8
Sept.	Pelvic	100	77	23.0

[a] Abbreviations: R. P. = right pectoral, L. P. = left pectoral, S. D. = soft dorsal, H. D. = hard dorsal.

other causes were insignificant. We have seen, however, that mortalities among other groups of both marked and unmarked bluegills ranged both higher and lower than for fish marked for this experiment.

Spawning Success

All populations produced large broods in 1961 and 1963, but all suffered spawning failures in 1962. The failures may have been due to predation of their own eggs by an underfed, overcrowded population of bluegills, as observed by Swingle & Smith (1943), or possibly caused by lower water temperatures in 1962. Late morning surface water temperatures in our ponds ranged from the high 60's to the high 70's (Fahrenheit) throughout the summer, rarely attaining 80° F., and then for only brief periods. For example, our weekly records show that the highest temperatures recorded in pond Kappa were 81.9° F. in 1961, 78.8 in 1962 and 81.9 in 1963. Following each of these highs the next temperatures recorded had fallen to 75° F. or below. Swingle (1949) stated that in Alabama ponds no young bluegills are produced until the temperatures of the surface waters reach 80° F. or above. However, Snow *et al.* (1960) reported that bluegills have spawned as early as late May in Wisconsin in water temperatures of approximately 67° F.

Our breeding stock came from a series of large flowage lakes located about 20 miles north of our study ponds, and in which the bluegills commonly spawn in late May or early June. However, 1-acre ponds are subject to greater fluctuations of water temperatures with changes in air temperatures than such larger lakes. The peak spawning period for our bluegills was believed to occur in the last half of June, and we suspect that this lateness was due to frequent, rapid cooling of these small water volumes by the frequent periods of cool weather that are common to northern Illinois in the summer. Lowest temperatures recorded in 1961 and 1963 from early June through July were 73.4 and 72.6° F. respectively. In 1962 a late morning temperature of 68.7° F. was recorded on July 16, with other June and July readings as low as 70° F. at mid-day. Since these temperatures were taken only once each week, we believe that interim, minimum temperatures probably fell into the middle 60's in all ponds at intervals in June and July, 1962. These frequent, sudden drops in temperature may have limited spawning in 1962.

Review and Discussion of Bluegill Data

We have four published listings of standing crops of bluegills when maintained as a single species (Table 15). These ranged in pounds per acre from 89.7 in a small Oregon pond to an estimate of 664 in an unfertilized 1.35-acre pond in Kentucky (Turner 1959). The highest standing crop reported in the Kentucky study for bluegills when in a mixed population was 547 pounds per acre. Both of these rather large poundages in Kentucky ponds were by estimates based on the return of marked fish when the pond was treated with rotenone. The highest bluegill poundage that we have seen recorded by Swingle (1950) was one containing 464.7 pounds per acre in a fertilized pond which also contained 49.4 pounds of largemouth bass. Bennett's (1954) highest recovery of bluegills per acre in his draining censuses of Ridge Lake was 193.3 pounds in 1947. Our highest standing crop of bluegills was 173.3 pounds per acre in the add-stock population in 1963, and the average of our four standing crops was 125.3. The comparative figures reveal the low fertility of our bluegill ponds.

Since the bluegill ponds were previously devoted to white crappies, we have some basis for comparing the relative efficiencies of the two species. In both instances Rho was the control pond, and fish were cropped from Lambda for transfer to Kappa. Tables 35 and 44 show that in all cases standing crops of bluegills exceeded those for white crappies. Maximums were 89.6 for crappies in the control pond Rho, and 173.3 for bluegills in the add-stock pond Kappa. A more legitimate comparison, however, might be that of the control ponds: 89.6 for crappies and 127.1 for bluegills. Greater productivity for the bluegill might be expected due to its greater fecundity and lower trophic level. It seems possible that the true differences may have been greater than indicated. There is strong evidence that the productivity of pond Rho declined over the period 1961–1963. If an equal decline occurred over the period 1958–1961, the differences in efficiencies of the two species would have been greater than indicated.

BROWN BULLHEADS

According to Forbes and Richardson (1920), the brown bullhead had an early but rather brief popularity as a commercial species in European ponds. Swingle (1957) developed procedures for its culture in Alabama ponds, but in later studies found the channel catfish to be more efficient and less subject to disease. Cross (1967) noted that the brown bullhead was propagated and distributed for use in ponds in Kansas in the 1950's but that the introduction was not a success. The species has apparently found small favor, and seems to have been very little studied. Brown bullheads were used in the present study because thriving populations of these fish of desirable size in postglacial lakes near our study area indicated that they might have some value for sport fishing.

Ponds Phi, Chi, and Psi (Unit 5) were completed in the fall of 1960 and first filled with water in the early spring of 1961. Between May 11 and June 23, 1961, each pond was stocked with 28 adults obtained by boat shocker from Fox Lake, in Lake County, Illinois. Weights stocked in each pond were similar, ranging from about 19 to 21 pounds. The control pond Psi was drained and censused at the end of the first and third growing seasons, and the companion ponds only at the end of the third. Although several interim estimates were made by conventional estimating procedures, some were so strongly in error that none have been used as standing crop data.

No fish were cropped in 1961, and when drained in October the control pond showed a "pounds gained" of 21.2 pounds and a final standing crop of 40.6 pounds. The pond was restocked with 19 adults and 7,882 young-of-the-year having a combined total weight of 33.5 pounds. In 1962 the cropped pond Phi was harvested of 61.9 pounds, of which 33.5 were transferred to pond

Chi. In addition, both ponds Chi and Psi were cropped in 1962 to thin what were believed to be excessive numbers of small bullheads. From pond Psi, 1,670 Age I fish (12.7 pounds) were removed in May and June, and 562 Age O (3.5 pounds) were removed in July and August. From pond Chi, 3,031 Age I fish (16 pounds) were removed in May and June, and 2,458 Age O (9.6 pounds) were removed in July and August. The only additional cropping was 35.4 pounds removed from the cropped pond Phi in 1963, of which 33 pounds were transferred to the add-stock pond Chi. As in adjacent Units 3 and 4, this unit was lightly fertilized in 1962 (Table 2).

Standing Crop Data

Table 41 presents the standing crop totals for four populations of brown bullheads, together with pounds of original stock, pounds gained, and other pertinent supplementary data. Table 42 presents the numbers in each age group and the percents of total numbers and weights of each group recovered in each draining census.

The cropped pond Phi had the smallest standing crop (16 pounds), but the highest pounds gained figure (91.9); the add-stock pond had the largest standing crop (90.2) and the lowest figure for pounds gained (29.8); the control pond ranked intermediate in both respects. Data from the control pond Psi indicates that this pond had a carrying capacity of between 40 and 50 pounds per acre. We may note that its final standing crop was 40.6 pounds when consisting of only two age groups in 1961, but increased to only 49.3 pounds when having the full complement of four age groups 2 years later (1963). At the same time, however, the final standing crop of the add-stock pond was almost twice that of the control pond, and the fact that a substantial weight of fish flesh was produced in

Table 41. — Pounds of brown bullheads per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Phi, Chi, and Psi (Unit 5) for periods of 1, 2, and 3 years. All censuses were by pond drainage in the fall.

Unit	*Pond*	*Treatment*	*Year of Census*	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
5	Psi	Control	1961	1	19.4	40.6	0.0	0.0	+21.2
5	Psi	Control	1963	2	33.5	49.3	1.7	18.0	+32.1
5	Chi	Add-stock	1963	3	19.5	90.2	66.5	25.6	+29.8
5	Phi	Cropped	1963	3	21.4	16.0	0.0	97.3	+91.9

Table 42.—Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of brown bullheads in ponds Phi, Chi, and Psi (Unit 5), in years indicated.

Pond, Year of Census, Treatment[a]	*Total Number Censused in Each Age Group*				*Percent of Total Number Censused in Each Age Group*				*Percent of Total Weight Censused in Each Age Group*				*Total, All Age Groups*	
	0	I	II	Adults	0	I	II	Adults	0	I	II	Adults	Number	Pounds
Psi 1961 0	10,547	0	0	20	99.8	0.0	0.0	0.2	63.9	0.0	0.0	36.1	10,567	40.6
Psi 1963 0	640	23	325	6	64.4	2.3	32.7	0.6	6.5	1.6	84.6	7.2	994	49.3
Chi 1963 +	497	163	647	9	37.8	12.4	49.2	0.6	5.0	7.5	80.4	7.1	1,316	90.2
Phi 1963 —	1,065	1	29	6	96.7	0.1	2.6	0.6	33.1	0.6	37.5	28.8	1,101	16.0

[a] Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.

1963, in spite of the addition of stock, indicates that the pond's carrying capacity had not been exceeded. The principal gains were made by bullheads of Ages O and I, most of which had been spawned in the pond, while practically no growth was made by fish of Age II and older which were the primary ages transferred into this population. Thus the limiting level of competition created among the larger and older fishes (Ages II and above) had little apparent influence upon the younger and smaller fishes. Average growth of Age O bullheads in 1963 was in fact substantially larger in the add-stock than in either companion pond, due, presumably to a lesser abundance than in the companion ponds (Table 42). The add-stock pond was probably somewhat more fertile than either companion pond, but we believe that the combination of greater total numbers and a more optimum distribution of sizes of bullheads contributed substantially to its larger standing crop.

Growth and Condition

Table 43 shows growth of brown bullheads of known age in our ponds as determined by actual measurements at the times of the fall draining censuses. Growth of bullheads in general, and brown bullheads in particular, seems to have been very little studied. Our growths were quite similar to those few records available for this species from New York and Illinois, as summarized by Carlander (1950). Our brown bullheads had growths similar to the black bullheads in Clear Lake, Iowa (Forney 1955), but grew more slowly than black bullheads in Oklahoma waters (Houser & Collins 1962).

Rate of growth was closely related to abundance. For example, first year growth in the cropped population in 1963 was less than in the add-stock pond because, in spite of cropping, the group numbered 1,065 in the final census in the cropped pond as compared to only 497 in the add-stock population.

Table 43. — Growth of brown bullheads in ponds used for carrying capacity experiments on the McGraw Foundation grounds.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number Censused in Parentheses*		
				1st	2nd	3rd
Unit 5	Psi	1961	Control	1.8 (10,547)	. .	. .
Unit 5	Psi	1963	Control	2.2 (640)	4.5 (23)	6.8 (325)
Unit 5	Chi	1963	Add-stock	2.6 (497)	4.6 (163)	6.2 (647)
Unit 5	Phi	1963	Cropped	2.2 (1,065)	5.5 (1)	7.7 (29)

The dominant class by weight (Table 42), and that which best reflected treatments in both 1962 and 1963 was the class spawned in 1961. Fig. 10 presents seasonal changes in average length, average weight, and condition for this dominant brood over the 1962 and 1963 growing seasons. Values for the cropped pond tended to rank high, and those for the add-stock pond low. Rates of condition declined in all ponds throughout 1963, and the decline was approximately as great in the cropped as in either companion population in spite of its much greater gains in both length and weight. Average seasonal length increments for the 1961 brood in inches were 1.64 in the cropped population, 0.95 in the add-stock, and 0.41 in the control population. Weight increments averaged 0.08 pounds in the cropped pond, as compared to 0.022 in the add-stock pond. Somewhat surprisingly, in the control pond Psi, average weight of individuals in this brood was less at the end than at the start of the growing season, in spite of an average length increment of 0.41 inches. In our sample of May 1, 1963, 100 Age II fish had an average length of 6.36 inches and an average weight of 0.131 pounds. In our fall census in late September, 1963, a sample of 182 bullheads of this brood had an average length of 6.77 inches and an average weight of 0.127 pounds. The loss in weight was reflected in the decline of average condition from 5.1 in April-May to 4.1 in October.

The rather sharp increase in condition in early 1962 (Fig. 10) is explained by the fact that for a short time in the spring we used a supplemental feed as bait in an attempt to concentrate the fish and expedite seining. While not notably successful for this purpose, it caused a temporary increase in condition.

The curves in Fig. 10 show that average lengths, weights, and condition of the 1961 brood were higher in all populations in the first spring sample of 1963 than they had been in the fall of 1962, and that condition was at a peak in the early spring and declined steadily throughout the following summer. These data show that surprisingly large percentages of total annual growth were made between the fall and spring samples. Mean lengths and weights for our fall samples of the 1961 brood were based on fish collected between September 30 and October 13 from ponds Chi and Psi and between October 14 and 27 from pond Phi. Mean weights for the first sample of 1963 were from samples collected between April 21 and May 11 from all ponds. The samples showed that for pond Phi 17 percent of the length and 31 percent of the weight increments made in 1963 (between October, 1962 and October, 1963) occurred prior to our first spring sampling period of 1963. Corresponding figures were 29 and 53 percent for pond Chi, 24 and 100 percent for pond Psi. While a part of the increase in weight could have been

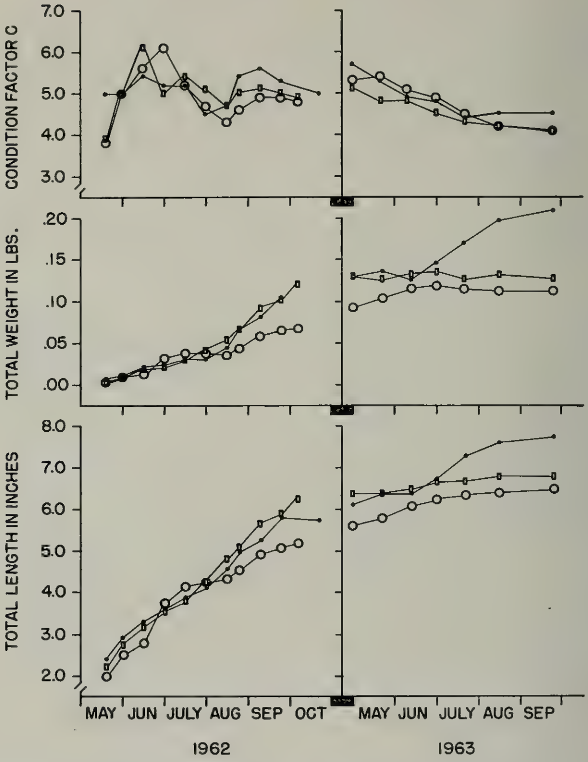

Fig. 10.—Length and weight increments and condition (C) of the 1961 year-class of brown bullheads in the control pond Psi (rectangles), add-stock pond Chi (circles), and cropped pond Phi (dots) during the 1962 and 1963 growing seasons.

due to gonadal development, lengths would not have been so affected.

Such overwinter growth was observed only among bullheads in our studies, and may be peculiar to this species. The fact that the bullheads had increased their lengths and weights, and were at their seasonal peak of condition in early spring suggests that they had found abundant food over much of the fall-to-spring period. Such a period of feeding and growth could conform with the seasonal fluctuation in abundance of some benthic fauna. As has been previously observed (Ball & Hayne 1952; Eggleton 1931; and others) invertebrate abundance (primarily midge larvae) typically increases in the fall to a mid-winter peak, and is followed by a continuous decline throughout the spring and summer and again increases in the fall. Exploitation of such a fall-to-spring abundance of invertebrate food could explain the pattern of growth by our bullheads. The spring-to-fall decline of the invertebrate population, coupled with increased competition from an abundant new year-class of bullheads, could explain the summer decline in growth and condition. It further implies small utilization or preference for the abundant crayfish, and little cannibalism by the larger and older bullheads.

Crayfish were abundant throughout 1962 and in the spring of 1963, and standing crops in pounds per acre in October, 1963 were 5.2, 6.2, and 38.8 in Phi, Chi, and Psi respectively. We had expected that the larger bullheads would make efficient gains on these abundant crayfish, and excretions by sampled fish indicated that the crayfish were commonly eaten. However, the fact that average size and condition of the original adult breeders actually declined over the 3-year course of the experiment indicates that crayfish were not heavily eaten, or were of little food value. It further suggests that competition for food among adults and Age II fish in 1963 may have been severe.

Mortalities

As in our previous presentations, mortality data are restricted to those groups for which both original and final numbers were exactly known. For bullheads we have data from only two year-classes — that of the original stock of 28 adults, and the 1961 brood, which was the only additional group present at drainage of the control pond in 1961 and the only group from which transfers were made. Because of their paucity, these data were not tabled but are presented here in the text.

Of the original 28 adults in the cropped pond Phi, 2 were removed in 1963 and 6 were recovered in the final census, representing a reduction of 20 individuals over the 3-year period, with a mortality rate of about 77 percent. Of the 28 adults stocked in the control pond Psi in May-June, 1961, 20 were recovered the following October, for a mortality rate of about 29 percent. For the 19 individuals restocked, mortality over the following two growing seasons was about 53 percent. Mortality was about 68 percent for 28 adults in the add-stock population over the full 3-year period, and 100 percent for the two adults transferred to this pond on August 13, 1963.

Mortalities among three groups of the 1961 brood by October, 1963 ranged from 6.5 percent for 200 bullheads transferred to pond Chi over the summer of 1963 to 94.8 percent for the 7,882 returned to the control pond Psi following the 1961 census. Mortality among 616 fish of this brood transferred in 1962 was 63.6 percent by October, 1963. The large mortalities recorded for the 1961 brood occurred during their second and third years when the fish ranged from 2 to 7 inches in total lengths. The absence of large cannibals among the 1961 brood, and the negligible growth and poor condition of the adult bullheads, indicate that cannibalism was not a major source of mortality. Since no large die-offs were observed, and sampled bullheads appeared to be healthy and vigorous at all times, the large mortalities among the 1961 brood appear to have been due to natural causes.

Spawning Success

New broods were produced in all ponds in all years, and reproduction was probably restricted to survivors of the original stock of adults. Table 42 shows that 10,547 Age O bullheads were recovered in the control pond in October, 1961, while recoveries of Age O bullheads in October 1963 ranged from a low of 497 in the add-stock population to 1,065 in the cropped pond. The numbers of Age O fish were highest where numbers of older fish were lowest, indicating a relationship to total density.

Review and Discussion of Brown Bullhead Data

No records of standing crops of brown bullheads could be found for comparison with ours, but we found four records from populations of single species of black bullheads which are listed in Table 15. All were from small Iowa ponds for which the standing crops were estimated by mark and recapture procedures or from the return of marked fish among those killed with rotenone. These estimated standing crops ranged from 128 to 653 pounds per acre, with an average for four populations of about 300 pounds per acre. It should be noted that this average was more than three times the maximum standing crop of brown bullheads produced in our ponds. It is also of interest that bullhead production ranked lowest for any species maintained in our ponds. We must therefore conclude that the Unit 5 ponds were not only extremely infertile, but probably afforded extremely poor habitat for this species.

Forbes & Richardson (1920) found that Illinois brown bullheads showed a preference for glacial lakes, lowland lakes, and larger rivers, in that order, and that they grew best in weedy ponds or quiet rivers. Trautman (1957) found Ohio specimens occurring most commonly in deep, clear ponds having some vegetation, preferring deeper water than either the yellow or black bullhead, and being less tolerant of turbid waters than the black bullhead. Limiting factors in our ponds probably included their small size and shallowness, the complete absence of weeds, and their moderate turbidity, which most commonly ranged 15-25 inches of Secchi disc visibility.

WHITE CRAPPIES

White crappies, although not one of the five principal species studied over the 3-year period 1961–1963, were used in two short-term experiments in ponds Kappa, Lambda, and Rho (Unit 4) in the period 1958–1960. The Unit 4 ponds had been completed in 1957, and in May of 1958 each pond was stocked with six male and five female white crappies in breeding condition. Lengths ranged from 7.2 to 9.3 inches, and total weight of the 11 fish released in each pond was about 3 pounds. All were collected by boat shocker from Fox Lake in Lake County, Illinois.

By early July of 1958 we became convinced that no fish remained alive in pond Lambda. Both ponds Lambda and Rho had been treated with rotenone on May 20, 1958 to remove green sunfish. Tests with live fish in cages indicated that both ponds were free of rotenone on May 27, and they were stocked with crappies on May 28. Despite evidence to the contrary, sufficient rotenone must have remained in pond Lambda to kill the breeding stock. Therefore, between July 7 and 22 1,750 young-of-the-year and 3 adults were transferred to Lambda from each companion pond so that Lambda received 3,500 young and 6 adults, having a total weight of about 4 pounds. There were no additional stock transfers, and all ponds were drained and censused in October.

All ponds were kept dry over the winter of 1958–1959 while a blanket of clay was spread over the base of the dams to help reduce seepage. Between May 7 and 14, 1959, each pond was stocked with 85 yearlings and from 10 to 12 adults, for a total weight in each pond of about 7.5 pounds. The yearlings were from our 1958 stock and the adults were new stock also obtained from Fox Lake. Over the 1959 and 1960 growing seasons pond Rho was maintained as a control and pond Kappa received crappies cropped and transferred from pond Lambda. Cropping was moderate in both years: 8.2 pounds in 1959, of which 7.9 pounds were released in Kappa and 22.8 pounds in 1960, of which 19.6 pounds were released in Kappa. All three ponds were drained and censused in October, 1960.

Standing Crop Data

Table 44 presents the standing crop totals for six populations of white crappies, together with pounds of original

Table 44. — Pounds of white crappies per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Kappa, Lambda, and Rho, for periods indicated. All censuses were by pond drainage in the fall.

Unit	*Pond*	*Treatment*	*Year of Census*	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
4	Kappa	Control	1958	1	2.9	37.0[a]	0.0	4.2	+38.3
4	Lambda	Control	1958	½	9.2	43.4	0.0	0.0	+34.2
4	Rho	Control	1958	1	3.0	35.5	0.0	4.2	+36.7
4	Kappa	Add-stock	1960	2	7.5	69.7	27.2	0.0	+35.0
4	Lambda	Cropped	1960	2	7.5	64.5	0.0	30.5	+87.5
4	Rho	Control	1960	2	7.5	89.6	0.0	0.0	+82.1

[a] This poundage is low because continuous losses of water through seepage reduced the area of this pond below that of the other two. If corrected, standing crop in pounds per acre in Kappa probably would have approximated that of pond Lambda.

stock, pounds gained, and other pertinent supplementary data. Table 45 presents the numbers in each age group and the percents of total numbers and weights of each group recovered in each draining census.

Actual standing crops in 1958 were 37, 43.4, and 35.5 pounds of crappies in ponds Kappa, Lambda, and Rho, respectively. However, since pond Rho had a greater loss of water through seepage, and an increasingly smaller pond area, its actual production in terms of pounds per acre was probably quite similar to that of pond Lambda.

Of special interest is the fact that pond Lambda, restocked in mid-July, produced the largest standing crop. From final census data it was clear that both weight and numbers of fish stocked in Lambda in July were only small percentages of those existing in the two companion ponds at that date. It is also clear that this smaller midsummer stock had only about one-half of the growing season in which to surpass total production in the companion ponds. Three possible explanations may be suggested:

1. Pond Lambda was much the most productive; or
2. The lesser abundance in pond Lambda permitted a more efficient conversion of available food; or
3. In the absence of fish there had been an accumulation of food which imparted a marked advantage when fish were stocked in mid-July.

Since no environmental differences were observed which would indicate a greater productivity for pond Lambda, we are inclined to favor the second and/or third of these possibilities. It may have been a combination of the two, either of which could have important connotations.

Also of interest is the fact that 3,140 of the mid-July stock of 3,500 in pond Lambda were recovered in October. This was a survival of about 90 percent which seems unusually high for fish of

Table 45. — Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of white crappies in ponds Kappa, Lambda, and Rho (Unit 4) in years indicated.

Pond, Year of Census, Treatment[a]	Total Number Censused in Each Age Group				Percent of Total Number Censused in Each Age Group				Percent of Total Weight Censused in Each Age Group				Total, All Age Groups	
	0	I	II	III & up	0	I	II	III & up	0	I	II	III & up	Number	Pounds
K 1958 0	8,904	0	0	4	99.9	0.0	0.0	tr	94.0	0.0	0.0	6.0	8,908	37.0
L 1958 0	3,140	0	0	5	99.9	0.0	0.0	tr	95.0	0.0	0.0	5.0	3,145	43.4
R 1958 0	37,006	0	0	4	99.9	0.0	0.0	tr	92.0	0.0	0.0	8.0	37,010	35.5
K 1960 +	0	4,134	60	6	0.0	98.4	1.4	0.2	0.0	91.0	6.0	3.0	4,190	69.7
L 1960 —	0	2,789	37	6	0.0	98.5	1.3	0.1	0.0	90.0	6.0	4.0	2,832	64.5
R 1960 0	485	2,013	106	9	18.6	77.0	4.0	0.3	0.0	80.0	16.0	4.0	2,613	89.6

Ponds are designated as: K = Kappa, L = Lambda, and R = Rho. Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.

this age. A high availability of accumulated food may have influenced survival.

Over the period 1959–1960 the actual production of fish flesh (pounds gained) was lowest (35 pounds) in the pond which received additions of stock, but only slightly higher in the cropped pond (87.5 pounds) than in the control pond (82.1 pounds). At the same time standing crops were similar in the cropped and add-stock ponds at 64.5 and 69.7 pounds respectively, but considerably the highest (89.6 pounds) in the control pond. These data suggest that 1) ponds Kappa (add-stock) and Lambda (cropped) were similar in their potentials, and that "pounds gained" were high (87.5 pounds in Lambda) or low (35 pounds in Kappa) in order to attain the presumed carrying capacity of 65–70 pounds, and 2) the control pond Rho, with its relatively large pounds gained figure and a final standing crop higher than that of the add-stock pond Kappa, had a considerably higher productivity than either companion pond.

While both of these observations may be true, there were differences in total densities and in the size and age structures of the populations that probably had some influence upon production. All populations produced strong year-classes in 1959, but in 1960 young were recovered only from pond Rho. The low production (pounds gained) of crappies in pond Kappa was associated with the largest total number of fish (4,200) but the poorest distribution of sizes and ages, with over 98 percent by numbers and 91 percent by weight concentrated in Age I over a length range of only about 2.5 inches (2.5–5). The high production in pond Rho was associated with the smallest total number of fish in the final census (2,613), with the fish more evenly distributed in three age groups (O, I, and II) over a length range of about 6.3 inches (1.7–8). We may note also in Table 46 that growth of all ages of crappies was fastest in the control pond Rho.

Table 46.—Growth of white crappies in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on white crappies in other Illinois waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Approximate Number of Fish Censused in Parentheses* 1st	2nd	3rd
Unit 4	Kappa	1958	None	2.4 (8, 904)	..	..
Unit 4	Lambda	1958	None	3.2 (3,140)	..	..
Unit 4	Rho	1958	None	1.4 (37,006)	..	..
Unit 4	Kappa	1960	Add-stock	.. (0)	3.4 (4,134)	5.9 (60)
Unit 4	Lambda	1960	Cropped	.. (0)	3.8 (2,789)	6.3 (37)
Unit 4	Rho	1960	Control	2.8 (485)	4.5 (2,013)	7.0 (106)
Other Illinois Waters	*Author*					
Ramsey Lake	Stinauer (1966)			3.8	6.6	8.6
Red Hills Lake	Price (1966)			4.2	7.5	9.8
Lake Decatur	Hansen (1951)			..	7.3	9.1
Lake Chautauqua	Starrett & Fritz (1965)			..	7.5	9.3

We may again observe the association of the greatest weight of fish with the smallest numbers. This may simply have been an expression of a greater natural productivity of pond Rho in 1960; however, it may be recalled that the same phenomenon occurred in the 1958 populations, but in different ponds. On the earlier occasion pond Lambda, restocked in mid-July with a much smaller population, made a greater total production by October than either companion pond. As suggested in the earlier section devoted to bluegills, such data may indicate that there is an optimum density which contains sufficient digestive tracts to make efficient use of available foods, but which is not so abundant as to be self-inhibiting in growth.

In the crappie data we must also consider the possible influence of contaminating fishes, and the rather large differences in standing crops of tadpoles and crayfish. Table 47 shows abundances of fish and the associated forms. Green sunfish, *Lepomis cyanellus* Rafinesque, represent the only contamination of consequence encountered in these studies, other than that, previously described, in the largemouth bass ponds.

Table 47.—Standing crops of white crappies, crayfish, and tadpoles, and relative abundances of Chara in ponds Kappa, Lambda, and Rho at times of the draining censuses in 1958 and 1960.

Pond and Year	*Standing Crop, Pounds Per Acre* White Crappie	Crayfish	Tadpoles	*Relative Abundance of Chara*
Kappa, 1958[a]	37.0	0.0	Trace	None
Lambda, 1958	43.4	0.0	90.0	None
Rho, 1958	35.5	0.0	75.1	None
Kappa, 1960	69.7	127.7	92.1	None
Lambda, 1960	64.5	69.0	241.3	Medium
Rho, 1960	89.6	Trace	205.1	Heavy

[a] Also contained 7.0 pounds of green sunfish in this census.

This contamination was limited to 2 adult and approximately 800 young green sunfish (total weight, 7 pounds) recovered in the draining census of pond Kappa in 1960. There is some question, of course, as to whether the presence of the green sunfish may have increased or inhibited production of crappies. In this case the contaminants were small enough to have provided forage for the crappies, but too small to have preyed upon crappies. It is doubtful that competition was great, or that absence of the 7 pounds of green sunfish would have permitted production of 7 additional pounds of crappies. It seems likely that the rather small weight of green sunfish had little influence upon crappie production.

There is little known basis for evaluating the influence of differing weights of tadpoles and crayfish upon fish production. Both would probably contribute to the production of largemouth bass, but might inhibit production of such less predatious forms as bluegills or small crappies. While small tadpoles or crayfish might be eaten by bluegills or crappies, larger forms might offer competition. Although the competition might not be direct, one must suspect that production of a large weight of crayfish, and/or tadpoles must divert energy that might otherwise contribute to fish production. Crayfish might have a secondary influence when so abundant as to eliminate weeds or algae. Evaluation may be additionally complicated by the sudden death or disappearance of these forms. We have observed large die-offs of crayfish for reasons unknown. Tadpoles may transform sooner in one pond than in another so that ponds yielding greatly disparate weights at time of census may have had similar weights one week earlier. So the importance of these forms is difficult to evaluate in the light of present knowledge. However, there are several associations to be noted in Table 47. Densities of vegetation (chara) in these ponds at the time of final census in 1963 were inversely correlated with standing crops of crayfish — about 128 pounds of crayfish with no chara, 69 pounds with "medium" chara, and only a trace of crayfish where chara was heavy. The degree of control seemed related to density of crayfish, and such control could have considerable influence upon a pond's ecology. In this instance the highest production of crappies was associated with a scarcity of crayfish and the densest stand of chara.

In the 1958 census of these ponds neither crayfish nor vegetation of any type were present. In that year the highest production of fish was associated with the greatest standing crop of tadpoles.

Growth and Condition

White crappie broods were not given distinctive fin clips as were those of our other species, and ages were assigned on the basis of length frequency distributions. Thus, ages of crappies were less precisely known than those of our other species, but probably sufficiently so for the comparisons offered in Table 46. These data show that growth of white crappies as single species in our infertile ponds was slower than growth made by crappies from mixed populations in other Illinois waters with which they are compared (Table 46). Totals cropped and transferred were too small to alter the original differences in densities. The control pond, Rho, with the fewest fish older than Age O in the final census of 1960 (Table 45), had the largest 2- and 3-year old fish in that year, and pond Kappa, with the largest numbers, had the smallest fish of these ages (Table 46). This is further shown by comparative length increments made by Age I fish in 1960. Based on average lengths of samples collected in June and October, length increments were highest (1.59 inches) in the pond having the least density of fish (Rho) and lowest (1.09 inches) in the pond having the highest density of stock (Kappa).

Samples taken during the growing season were too few and too small to provide seasonal curves for growth and condition for these populations, but we may compare conditions of a few fish from each pond at the time of final censuses: 21 from Kappa ranging from 4 to 11 inches in length, 25 from Lambda from 6 to 10 inches long, and 80 from Rho from 6 to 12 inches long. Conditions in the add-stock pond Kappa averaged low (3.5), the cropped pond high (4.3), and the control pond intermediate (3.9). These rankings, however, did not conform with those of rates of growth, which were intermediate in the cropped pond with its denser population and high in the control pond with the lower population density (Table 46). As with some of our earlier species, rates of condition would here be poor indicators of comparative rates of linear growth.

Mortalities

We have already mentioned the remarkably low mortality among the Age O crappies that were transferred from ponds Kappa and Rho to pond Lambda in mid-July, 1958. When censused on October 1, 3,140 of the original 3,500 were recovered, a mortality of only about 10 percent over an approximately 2½-month period. Mortality of adults over the same period was 3 of 8, or about 37 percent.

The crappie broods were not identified by distinctive clips as were those of our other species, and data for crappies is therefore limited. Our only additional data were derived from an attempt in 1960 to measure seasonal rates of mortalities for Age I crappies given a distinctive fin clip for each of the three summer months. Approximately 100 were marked in each pond in June, July, and August, and returns were counted in the October census. The results were extremely erratic and indicated that mortalities from handling and marking were sometimes large and subject to large variations. For example, mortalities by October of Age I crappies were 77, 67, and 47 percent for those marked in June, 98, 100, and 43 percent for those marked in July, and 98, 100, and 93 percent for those marked in August, in ponds Kappa, Lambda, and Rho respectively.

Spawning Success

Reproduction was successful in ponds Kappa and Rho in 1958 and was absent in pond Lambda due to the elimination of brood stock by rotenone. Recoveries in October of young spawned in these ponds were 37,006 from pond Rho and 8,904 from pond Kappa. We have no knowledge of what caused such a wide difference in numbers of young produced in 1958.

Numbers of Age I crappies recovered in the 1960 census (Table 45) show that all three populations produced moderately large broods in 1959. In 1960, however, young-of-the-year were recovered only from pond Rho. Environmental factors which also showed marked variations in these ponds in 1960 were the abundances of older crappies, and the abundances of crayfish and chara. Age O crappies were present 1) where numbers of older crappies, particularly those of Age I, were least abundant (Table 45), 2) where crayfish were absent, and 3) where chara was the most abundant. Thus, the absence of Age O crappies in the two companion ponds may have been due to greater predation by greater numbers of older fish in waters having less chara and less protective cover. Predation of eggs or larvae of crappies by the abundant crayfish populations might also have been a factor.

Review and Discussion of White Crappie Data

The white crappie has been found to be undesirable in small ponds (Hall *et al.* 1954; Jenkins 1958; and others) because of overcrowding and slow growth. So far as is known it has not previously been used as a single species, but has produced large poundages in mixed populations. Jenkins (1958) reported an average standing crop of 72 pounds per acre of white crappies in mixed populations in 18 Oklahoma ponds, and a maximum standing crop of 205 pounds per acre when combined with black bullheads (107 pounds per acre) and mixed sunfishes (15 pounds per acre). The species finds its greatest value as a sport fish in larger lakes and reservoirs where catch rates are sometimes quite high. Buck & Cross (1951) reported a large catch from a 5,000-acre Oklahoma reservoir where the crappies were attracted by a temperature gradient. Over a 69-day period in late winter the hook-and-line catch totaled 626,897 crappies weighing 194,338 pounds which computed to approximately 39 pounds per acre for the entire 5,000 acres. A majority of this total was removed from a single cove in which the entrance of warmer water was creating a mild temperature gradient. Total catch from this 3-acre cove over the 69-day period was at a rate of over 22 tons per acre, practically all from a single year-class.

In an earlier section we noted that subsequent stocking of bluegills in these same ponds (Kappa, Lambda, and Rho) produced considerably larger standing crops than had been obtained from white crappies. Maximum standing crops in pounds per acre were 89.6 for crappies and 173.3 for bluegills. Comparing only control ponds, the poundages were 89.6 for crappies and 127.1 for bluegills. Such a difference indicates a lesser efficiency for white crappies, due probably to their subsistence at a higher trophic level.

As earlier observed for bluegills when stocked in the same unit of ponds, highest total production of crappies was not made in the pond containing the most fish. This encourages the speculation that there is an optimum density for maximum production. This optimum number would include enough individuals of proper sizes to obtain efficient utilization of the pond's resources, but they would not be so abundant as to stunt their own growth. We must also recognize that maximum production of fishes is dependent on high production of their invertebrate foods. Maximum production of invertebrates would occur under an optimum rate of exploitation. The optimum density of fishes might in some cases be that which provides optimum cropping and maximum production of the invertebrates used as food. Such optimum synchronization would result in maximum fish production. Variations in the degree of synchronization would produce variations in fish production.

GENERAL DISCUSSION

Table 48 summarizes standing crop data presented in earlier sections. For each species it includes an average standing crop for all ponds receiving each treatment, and in the last column an average for all populations in all seasons, regardless of treatment. In this last column of the table we can observe that standing crops of bluegills narrowly exceeded those for yellow perch, which were followed by smallmouth bass, largemouth bass, white crappies, and brown bullheads in that order. We must emphasize, however, that because of differences in environments this order of rank does not necessarily reflect the relative efficiencies of these species. Its principal value is to indicate the potential for variation in standing crops of the individual species. Direct comparisons between species have been limited to those instances where standing crops of two different species were measured in the same ponds in consecutive years. As detailed earlier, such comparisons indicated that smallmouth bass were more efficient than largemouth bass, that yellow perch produced larger poundages than either largemouths or smallmouths, and that weights of bluegills were larger than those earlier produced by white crappies in the same ponds.

Table 48. — Average standing crops (rounded) in pounds per acre for the six species of warmwater fishes studied as single species in 1-acre ponds, 1957-1963.

Species	*Standing Crop for All Ponds Receiving Each Treatment*			*Overall Average, All Populations*
	Control	Cropped	Add-stock	
Bluegills	114	101	173	125
Yellow Perch	98	122	184	124
Smallmouth Bass	88	46	150	93
Largemouth Bass	71	51	90	71
White Crappies	51	65	70	57
Brown Bullheads	45	16	90	49

Three sources of variation in our standing crops were: 1) differences in experimental treatments received, 2) differences in pond fertilities, and 3) differences in size and age composition of the populations. All species were generally responsive to cropping, or to the additions of stock, although the influences of the treatments were sometimes masked by differences in pond fertilities or in population compositions. As a general rule, however, standing crops were highest and rates of production (pounds gained) were lowest in those populations receiving additions of stock, standing crops were lowest and rate of production highest in cropped populations, and both values tended to be intermediate in the control populations. A primary effect of the experimental treatments was to create three differing levels of fish density for each species. In general, rates of growth and condition were poorest, rates of reproduction were lowest, and rates of mortality were highest in those populations having the greatest densities of stock.

The areas for greatest individuality among species were probably those of age and size structure of the populations and the influence of the differing structures upon production. Some species exhibited characteristics or relationships that were either unique to that species or less evident among the others and therefore it might be appropriate to briefly review these, making comparisons between species where useful.

In terms of efficient use of available food supplies, and the ability to sustain a high rate of production, it appears that the smallmouth bass was the most successful as a single species of any of the six species studied. We found it to be extremely hardy even when subjected to marking and frequent handling in seines and live boxes. It reproduced adequately under a variety of conditions, including ponds with bottoms of hard clay overlayed by claysilt, and in the absence of sand, rocks, or gravel. From original stocks as small as 5.6 pounds per acre (including some spawning adults), maximum standing crops were achieved in two growing seasons if successful reproduction occurred in both seasons. From original stocks approximating one-half of the carrying capacity of the ponds, maximum standing crops were achieved in a single season with only one successful reproduction period. Standing crops as high as 170–180 pounds per acre exceeded those of the largemouth bass (later used in the same ponds) by as much as 40–50 pounds per acre. The greater production of the smallmouth bass over that of the largemouth was attributed primarily to the more efficient utilization of lesser invertebrates as food by smallmouth of larger sizes. Our heaviest populations of smallmouth were those dominated by 6- to

11-inch individuals, and these larger fish seemed as efficient in utilizing the small invertebrates as were the young-of-the-year. In contrast, standing crops of largemouth bass declined progressively as the populations became increasingly dominated by largemouth of these same intermediate sizes. The smallmouth was unique in that high production was not dependent upon large numbers of both small and large fish. Data from Unit 1 indicated that when sufficient numbers were present to make efficient use of an abundance of invertebrates, size of the bass was relatively unimportant, and the absence of young, small fish might cause little or no loss in total production of fish flesh. When larger fish (about 11 inches and above) were present, however, their growth was inhibited when neither crayfish nor smaller bass were available as prey.

Standing crops of smallmouth bass measured in the fall exceeded those estimated in the spring. For the control and add-stock populations in Unit 4, three standing crops estimated in the spring ranged from 55.4 to 64.5 pounds per acre, averaging 58.8 pounds and three measured in the fall ranged from 84.9 to 95.5, averaging 91.2 pounds. Thus the spring standing crops averaged only about 64 percent as large as those measured in the fall. When numbers of bass were large, as in the add-stock populations, reductions to the spring levels were brought about by large overwinter mortalities, chiefly among the older and larger individuals. Where fish were less abundant, as in the control pond, the low spring level was due more to a failure of the older individuals to add flesh, in spite of large reductions made in their numbers, and their having eaten major portions of the smaller members of the population. Carrying capacities were higher in Unit 4 ponds in the fall of the third season than at any previous time due to improved fertility and greater food production in the ponds. Higher standing crops at this time were believed also due in part to a more optimum distribution of sizes and ages in the population than when formerly dominated by older and larger individuals of the 1958 brood.

Manipulations of stock produced differing levels of population densities, and these influenced the populations in a number of important ways. In general, rates of growth and condition were poorest, rates of reproduction were lowest, and rates of mortality were highest in those populations having the greatest densities of stock. Fastest rates of growth, however, were not always accompanied by highest rates of condition, and comparative rates of either frequently were poor indicators of comparative rates of the other.

Our largest standing crops, and presumably our most efficient populations of largemouth were those containing large numbers of both small and large fish. We believe that when largemouth populations contained few or inadequate numbers of young-of-the-year, the pond's carrying capacity was not attained and much of the pond's resources remained unutilized.

Our data from Unit 2 ponds provided evidence that when cropped at a proper rate largemouth populations are capable of a seasonal replacement of fish flesh equal to the poundage that the pond can support. Although we obtained no tangible evidence of such a replacement potential among our smallmouth populations, we believe that such failure was due primarily to our experimental procedures. The replacement potential of smallmouth in our ponds was not adequately tested by proper cropping, but the large standing crops and large gains made in uncropped ponds indicated that such a potential did exist. We suspect that the replacement ability of cropped populations of smallmouth would be at least equal to that of the largemouth.

The largemouth bass has been quite widely used as a single species in ponds, and probably considerably more so than the smallmouth. When so used, the largemouth has sometimes failed to sustain itself due to failures of reproduction, or of survival of young, and this is believed to be a common failing. In the present experiments, however, young-of-the-year were present in all of 10 largemouth populations and 10 of 11 smallmouth populations at the time of the final censuses. We believe that our data show both species to be capable of a high sustained production as a single species in 1-acre ponds, and especially so when subjected to cropping. Since bluegills are also known to frequently overpopulate and to eliminate reproduction among coexisting bass, we believe that the chances for a sustained production of bass are as good when stocked alone as when mixed with bluegills.

Absence of a forage species for either of the basses has certain disadvantages. In our populations coefficients of condition were generally poor, fish were never fat, and growth of fish older than Age O was usually slower than for bass in mixed populations. On the other hand, our bass populations indicate that total weights of bass actually could be larger when a bass species is alone than when it is in a mixed population. In addition to their greater total weight and number, bass as single species would, in most cases, be more readily caught than when better fed through preying upon a companion species. As mentioned before, Bond and his associates in Oregon (personal communication) found bass fishing to be much superior in ponds where the bass were alone than when they were associated with bluegills. If a pond owner is primarily interested in bass, use of either bass species could prove rewarding. In our experience, however, we would have a slight preference for the smallmouth because it better withstood marking and frequent handling, suffered fewer mortalities, and was more able to subsist on an invertebrate diet.

So far as is known, the yellow perch has not previously been stocked as a single species, and no standing crop data are available for comparison with ours. The species can, however, attain large numbers and weights when in combination with other species in fertile waters. In 1920, the 10,000-acre Lake Mendota in Wisconsin was estimated to contain 15,000,000 adult perch (Hasler & Wisby 1958) which, using the average weight of adults caught at that time, projects to a standing crop of about 169 pounds per acre of adult perch only. Moyle *et al.* (1950) have recorded estimates as high as 184 pounds per acre in Minnesota game fish lakes, although the mean for 41 such lakes was only 32.1 pounds per acre. Our highest standing crop was 192 pounds per acre as a single species in pond Alpha, which only slightly exceeds the maximums estimated for perch in multispecies populations. These data suggest that the perch may be particularly well adapted to its own ecological niche, and relatively little affected by competition from companion species.

Perch growth was generally fastest in our cropped population and slowest in our add-stock population, and closely related to density of stock. There was strong evidence, however, that intrabrood density was more critical or controlling than total population density, with little apparent competition between perch of different ages or sizes. For example, perch of the 1962 brood in the add-stock population grew faster than their more numerous counterparts in the control population in spite of the much greater total weight (all age groups combined) of perch in the add-stock population. It was further notable that at the time of the final census in 1963, 2,861 perch of this 1962 brood had an average length (4.7 inches) only about 0.4 inch less than that (5.1) of 728 perch of the 1960 brood that had survived from the original stocking of October, 1960. The 1962 brood of perch had made an average length increment of about 3.5 inches in its first year and 1.2 inches in its second year, while the 1960 brood had made a length increment of less than 1 inch over the entire 2-year period.

It should be pointed out that numbers of perch older than the 1962 brood were being continuously augmented by perch transferred from the cropped pond Zeta. However, the total of all perch older than the 1962 brood in the 1963 census numbered only 1,012 as compared to the 2,861 in the faster-growing 1962 brood. While the older perch of the 1960 year-class had apparently attained a growth limit due to intraclass competition for some element within the environment (probably food), they obviously were offering little competition to the much more abundant and faster-growing perch of the 1962 brood. We had at the same time a small group of "cannibal" perch of the 1960 year-class that made excellent growth due to their cannibalistic tendencies. So we had within the add-stock population three distinct groups of perch, probably with different food habits, and which offered relatively little competition to each other: 1) the large, fast-growing cannibals of the 1960 brood, 2) the more abundant perch of the 1960 brood that had attained their growth plateau, obviously subsisting upon an invertebrate diet, but of a different composition than that utilized by the younger perch, and 3) the younger, most abundant and fastest-growing group in the population, which obviously utilized foods not taken by the older fish, and which permitted them to literally grow into the size range of perch that were 2 years older.

Some studies have shown the food habits of perch to change to some degree with increase in size. Tharratt (1959) found that immature insects were prominent as food for all size groups (2.5 inches and up) of perch in Saginaw Bay, but that mayfly nymphs, which were the largest insects available (presumably *Hexagenia* sp.), were found only in the stomachs of perch longer than 4.7 inches. Tharratt also found that copepods were the chief constituents in the food of young-of-the-year, but were absent from the stomachs of perch more than 5.4 inches long. On the other hand, Pearse & Achtenberg (1920) and Herman *et al.* (1959) have observed that adult perch commonly feed on cladocerans, utilizing gill rakers adapted to straining these small forms from the water. It therefore seems quite remarkable that in our studies one age group of perch could find sufficient food to grow well, while an older group of only slightly larger average size appeared to have done little more than subsist. We have previously noted that the nymphs of the larger burrowing mayfly, *Hexagenia limbata*, were apparently eliminated from the add-stock pond, while remaining abundant in the companion ponds. Possibly the 1960 brood in pond Theta had developed the habit of feeding almost exclusively on these mayflies and the perch were unable to change their feeding habits when this food was exhausted. The senior author observed a somewhat similar occurrence (unpublished) in which a large population of white bass in a large southern reservoir literally starved to death in a year when its principal food (gizzard shad) had a spawning failure, although other forage fishes of similar size were available.

The brown bullheads were used only in Unit 5 where they produced the lowest standing crops recorded in this study. We believe that this was because the Unit 5 ponds were the least fertile of our ponds, and because the brown bullheads were poorly adapted to our weedless, moderately turbid, moderately shallow ponds with their soft clay-silt bottoms. This poor adaptability was emphasized by the fact that survivors of the original stock of 28 adults failed to increase their average size over the 3-year period of study. There was no evidence of cannibalism in these populations. Although crayfish were usually abundant, and were known to be eaten by the larger bullheads, they obviously did not provide an adequate diet. With no cannibalism, food for all sizes of bullheads was limited primarily to invertebrates. It is therefore interesting that there was little apparent competition for food between the Age O fish and those older than Age O. As in the yellow perch populations, competition among bullheads was greater within than between age classes. In this instance Age O bullheads in the add-stock pond (most of the bullheads added were older ones) grew faster than their counterparts in the companion ponds because of their lesser abundance, even though the population of fish older than Age O was much larger in the add-stock than in either companion pond.

We earlier noted that production of bluegills was greater than that of white crappies earlier maintained in the same ponds. Our standing crops of bluegills were low by common standards (Table 35) due to the low fertility of the ponds in which they were stocked. However, the bluegills produced the highest average standing crops, and were probably the most efficient of any of our six species.

Both bluegills and white crappies were stocked in Unit 4, and both exhibited the phenomenon whereby a smaller number produced a greater weight than a larger number of the same species. We had observed that our cropped pond Lambda had a larger standing crop (weight) of bluegills than the control pond Rho even though the total population numbered less than one-sixth that of Rho at the time of census. Also, the same association was apparent in the white crappie populations in both 1958 and 1960, with that of 1958 being the most distinct. We may recall that in 1958 the population in pond Lambda was inadvertently destroyed by rotenone, and the pond was restocked in mid-July with a smaller weight and number than were present in either companion pond. By the time of the census in October this smaller number had produced a larger poundage than either companion pond in only about one-half as much time. The differences in standing crops could have been caused by differences in pond fertilities. If so, however, in the case of the crappies pond Lambda would have been enormously more fertile than pond Rho in one period and slightly less fertile in the other. Differences in age structures of the populations could also have had some influence. We recognize that there may be other possible explanations, one involving the concept of an optimum density. The effects of an optimum density might be asserted in at least two ways:

1. The density of fishes would be in optimum relation to that of their prey if feeding activities maintained the prey species at population levels at which they most efficiently replaced their own numbers. Thus the maximum food supply would be provided for the predator fishes. Too few fish would make inefficient use of the prey species, whereas too many would cause overexploitation and a temporary collapse of both predator and prey populations.

2. There may be an optimum density which contains enough fishes to make efficient use of available foods, but not so dense as to be self-inhibiting. We know that some fishes attain densities at which they may inhibit their own growth and reproduction. Even when the food supply is not a limiting factor, it may be possible for a smaller number of fish to attain a greater total weight than a larger population so dense that it created an inhibitory barrier. Such a barrier might be either physiological or psychological, and could be more limiting upon a species maintained alone than when the fish are in a mixed culture. It it known that certain combinations of species may be extremely compatible and that one may actually en-

hance production of the other. Data reported by Rose (1959) suggest the engaging possibility that when two unrelated or distantly related species are combined, one may have the effect of metabolizing away self-inhibiting products produced by the other.

The influence of total fish densities, of differing densities by size or age group, and the influence of such associated organisms as tadpoles and crayfish upon fish production are difficult to measure and evaluate in ponds, but may be of great importance. This may be especially true in single species populations. We have seen that in our control pond Rho the standing crops of bluegills, crayfish and tadpoles were all much higher in October, 1961 than in October, 1963. We must therefore wonder if the carrying capacity of pond Rho declined so markedly over that period, or if the greater production of bluegills in 1961 was in some way enhanced by the greater numbers of crayfish and/or tadpoles.

Whether it may or may not be influenced by an inhibitory factor, an optimum density will exist for each population. In its simplest terms, the amount of new flesh produced in a population is dependent upon three things: 1) the carrying capacity of the pond for that species, 2) the number and weight of fish already present, and 3) the pounds being cropped (or otherwise removed) that are subject to replacement. If the carrying capacity has been attained, and no fish die or are otherwise removed, the fish cannot grow and no new flesh can be produced. On the other hand, the more pounds cropped the more that can be produced in replacement. The most efficient and productive arrangement will be one in which the optimum number is cropped, maintaining the population continuously below carrying capacity but not reducing the number of fish below the level that can by growth and recruitment efficiently replace those removed, as was done in two of our smallmouth populations. As indicated by studies of smallmouth bass (Bennett & Childers 1957) and by our largemouth experiments in Unit 2, under an optimum rate of cropping it may be possible to remove more pounds in a season than the pond can support at any time. For each pond there must exist an optimum population density, and an optimum rate of cropping, and these will differ and fluctuate as the productive potential of individual ponds must also differ and fluctuate. The rates of production to be obtained will be the result of the interaction of these complex and unstable forces, and the efficiency of production will be determined by how nearly the optimum rates of cropping and density can be maintained.

A primary purpose of this investigation was to consider the relationship of carrying capacity to standing crop. In doing so we should again clarify our usage of the two terms. Standing crop is universally recognized as the quantity of organisms present at the particular time of measurement, and is so used here. As defined by Krumholz *et al.* (1957), carrying capacity was considered to be that quantity surviving through the least favorable environmental conditions over a stated interval of time. By such terms it automatically becomes a minimum quantity. There are, however, many practical reasons for measuring maximum rather than minimum levels of abundance. Many researchers and commercial fish growers refer to their maximum standing crops as the carrying capacity of the unit involved. They interpret this to mean the maximum poundage that the pond can produce, or support, of the number and type of organisms involved, and under the environmental conditions that existed or were maintained. This usage is now very widely accepted. For our present purposes we have recognized what was termed a temporary carrying capacity by Edwards & Fowle (1955).

We have measured standing crops in both spring and fall and have evaluated these in terms of carrying capacities, recognizing that the poundage of fish supported by a pond in late winter or early spring may be quite different from the poundage that the same unit might support in late summer or fall.

In evaluating carrying capacity it is important to come to an understanding of its relative stability. Carrying capacity is sometimes conceived as being a relatively stable quantity, changing little from year to year. This is tantamount to saying that the environment itself is not subject to change. We recognize a number of factors other than changes in the environment as being capable of influencing the standing crop, but we believe that our data have shown that the pond environments were relatively unstable, and that variations in standing crops were frequently due to changes in the environments and in the ponds' carrying capacities.

Changes in carrying capacities of the ponds were believed to have had two principal causes: 1) changes in such physical elements of the environment as inorganic fertility, turbidity, or type and density of vegetation, and 2) changes in densities of associated invertebrates, including those utilized as food, such as scuds or mayfly nymphs, or those having a potential for either inhibiting or enhancing the production of fish, such as crayfish.

In working with our data, standing crops frequently were judged to have been either larger or smaller than the pond's carrying capacity. When larger, it was because of excessive additions of stock, and the excess was indicated by a loss in the pounds gained or lost column. We could not, of course, know when the point of equilibrium was reached and when additional losses would or would not occur. However, when a loss had occurred, and when additions of stock had been quite continuous up to near the time of census, we assumed that equalization was still in progress and that the standing crop probably still exceeded the pond's carrying capacity. It was more difficult to make a judgment as to when the standing crop was at or below the pond's carrying capacity. If the standing crop was medium to large, the pounds gained not overly large, and the population structure reasonably normal, we felt that the standing crop probably approximated carrying capacity. If the pounds gained figure was unusually large the question arose as to whether the carrying capacity was also unusually large and may not yet have been attained. We suspected our standing crops to be below carrying capacity when they were small and when total numbers of fish were small, or when one or more size or age groups of the population were inordinately small, or absent, due either to heavy cropping, excessive cannibalism, or reproductive failures. Among smallmouth bass, however, we found that absence of Age O fish was of little importance if a sufficient number of intermediate sized smallmouth were available to make efficient use of the invertebrate food supply.

While the standing crop is not necessarily a measure of carrying capacity the two are intimately related, and the former is limited by the latter. Both must be considered dynamic quantities dependent upon the interaction of all forces within the environment. As an expression of these forces, carrying capacity must also fluctuate, and can have no greater stability than that of the environment. As a finite quantity, carrying capacity may be extremely difficult to measure exactly, and might only by chance be the same at any two points in time. Standing crop might be conceived as the "tail on the kite," always tending to follow, either up or down, the movement of the controlling body.

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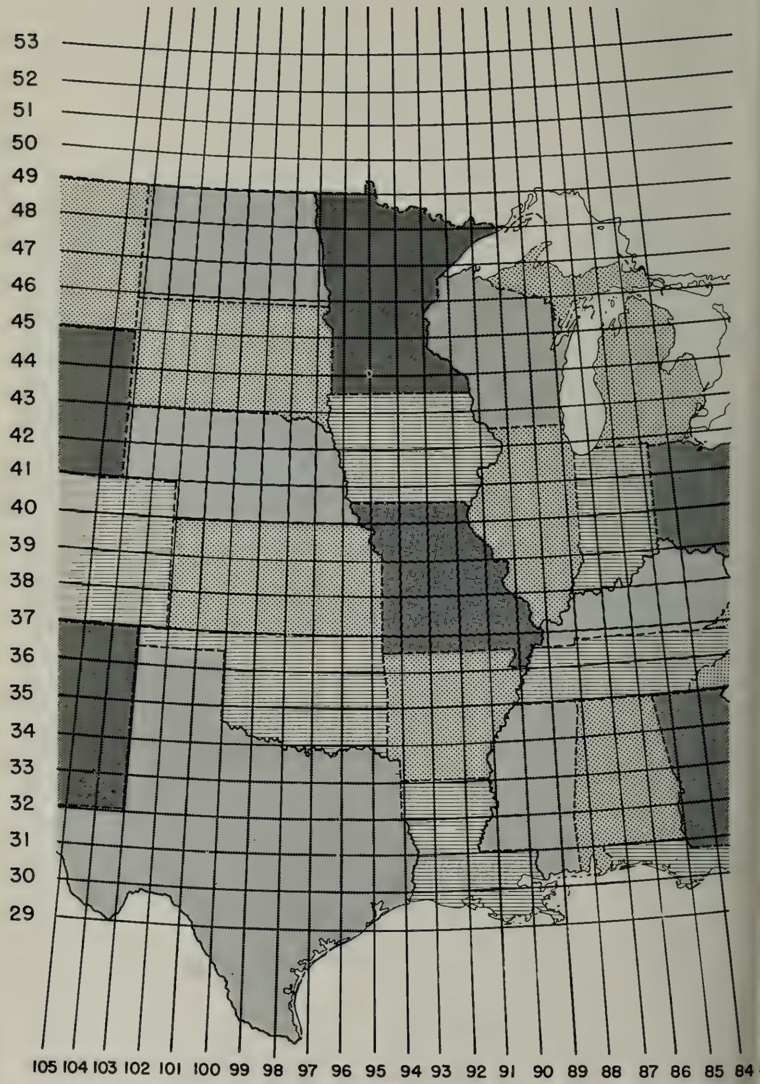

Frontispiece. — Map of central United States, including degrees of latitude and longitude as referred to in discussions of mallard and black duck band recoveries.

Migrational Behavior of Mallards and Black Ducks as Determined from Banding

Frank C. Bellrose
Robert D. Crompton

LARGE-SCALE BANDING of migratory ducks in the United States first occurred in Illinois. During the spring and fall of 1922, Frederick C. Lincoln of the U.S. Bureau of Biological Survey (now Bureau of Sport Fisheries and Wildlife) banded 1,670 mallards *(Anas platyrhynchos)* and 57 black ducks *(Anas rubripes)* at the Sanganois Duck Club, near Browning. In 1926, Lincoln again returned to the Illinois River to band 941 mallards and 27 black ducks near Bath.

We do not know why Lincoln selected this area of the nation to demonstrate the feasibility of trapping large numbers of waterfowl. It may have been because Illinois is about midway between the principal breeding and wintering grounds of the mallard, or because the state was known for its abundance of migrating mallards.

Illinois remains one of the leading states for migrating waterfowl in the nation; only a few states are frequented by larger numbers. And, as in earlier days, mallards are especially abundant. Weekly waterfowl censuses during the fall of 1965 revealed that mallards composed 65 percent of all ducks concentrated in the Illinois and Mississippi River valleys of Illinois. Before their decline in the 1950's, mallards formed an even larger proportion of the duck population. Peak numbers of mallards in these valleys have varied (1945–1966) from a high of 2,435,000 in 1955 to a low of 563,000 in 1961.

Because of the abundance and importance of mallards, this species has received the greatest attention in banding programs within the state. Prior to the entry of the Illinois Natural History Survey into the waterfowl banding program in 1939, the only large contribution to Lincoln's effort in Illinois was that of Chris Goetz. Between 1932 and 1940, he banded almost 5,000 mallards at the Duck Island Preserve near Banner in Fulton County, Illinois.

The principal duck banding program of the Survey extended from 1939 through 1952. Survey personnel have continued to band ducks, but since 1952 the bandings have been more experimental in nature, directed toward problems of homing and orientation. Nevertheless, many of the indirect recoveries from these experimental bandings can be used to analyze fall migration movements.

Personnel of the Illinois Department of Conservation and the U.S. Bureau of Sport Fisheries and Wildlife have also banded appreciable numbers of ducks in the state. To provide as much substance as possible to our analysis of duck bandings in Illinois, we have made use of band recoveries from the Department of Conservation's banding program at the Union County Wildlife Management Area, Ware, Illinois, and the Bureau's bandings as well as our own at the Lake Chautauqua National Wildlife Refuge, Havana, Mason County, Illinois, hereafter referred to as Lake Chautauqua.

To round out the analysis of mallard movements in the Mississippi Flyway, we have used band recoveries from mallards banded by the Bureau of Sport Fisheries and Wildlife at the Delta Marsh, Manitoba, Canada, and the Squaw Creek National Wildlife Refuge, Mound City, Missouri.

The objectives of the analysis presented in this paper were to determine: a) the migration patterns as shown by band recoveries from mallards and black ducks, b) the variation in migration patterns of mallards banded at various localities in the Mississippi Flyway, c) the degree of variation in migration patterns of mallards from year to year, d) the period of time mallards remain at a given area on the flyway, and e) the chronology of migration in the mallard as shown by band recoveries.

ACKNOWLEDGMENTS

We are most indebted to numerous persons for their contributions to this paper. Foremost are the many biologists who as students or recent college graduates banded thousands of ducks over the years at the several banding stations operated by the Natural History Survey.

The Survey banding program was initiated in 1939 by Arthur S. Hawkins, now with the Bureau of Sport Fisheries and Wildlife, and John M. Anderson, now with the National Audubon Society. Because of their enterprise, the program was successful in meeting early goals, and was continued in the pattern they initiated.

Robert Brough, in 1952 and 1953, hand tabulated most of the band recovery data received between 1939 and 1952, and, by so doing, made a major contribution to the analysis of data in this paper. Dr. William Starrett, Aquatic Biologist with the Survey, suggested showing the longitudinal distribution of band recoveries by mean and standard deviation.

George Arthur, Waterfowl Biologist, Illinois Department of Conservation, kindly made recovery data available on mallards banded at the Union County Wildlife Management Area. Arthur S. Hawkins provided the mallard recovery data from bandings at Delta Marsh, Manitoba.

Through the efforts of Walter Crissey, Kahler Martinson, and Earl Baysinger of the Migratory Bird Population Center, Bureau of Sport Fisheries and Wildlife, computer tabulations were obtained of the mallard recoveries from bandings at the Squaw Creek National Wildlife Refuge near Mound City, Missouri. We are grateful to the several refuge managers at Squaw Creek who banded ducks there in the period 1937–1963.

John Chattin and Arthur S. Hawkins, Bureau of Sport Fisheries and Wildlife, reviewed the paper for its biological context. Dr. H. W. Norton, Department of Animal Science, University of Illinois, reviewed the paper for data analysis. O. F. Glissendorf, Technical Editor, and Dr. Glen C. Sanderson, Head, Section of Wildlife Research, Illinois Natural History Survey, edited the paper. Richard Sheets, Illustrator for the Survey, prepared the maps and graphs.

METHODS

Type of Traps

The basic trap used in Illinois to capture dabbling ducks was 16 feet long, 8 feet wide, and 6 feet high (Fig. 1). It had V-type entrances at either end, with a holding box at one end. This trap was used primarily to capture mallards and black ducks. Usually two to four of these traps were operated at each banding station.

The traps were placed in water 6–18 inches deep and baited with grain. Whole corn was usually used as bait for attracting mallards and black ducks.

Location of Banding Stations in Illinois

Personnel of the Illinois Natural History Survey banded ducks at five principal locations in the state — Lake Chautauqua, Mason County, 1939–1944, 1947–1952, 1954–1966; McGinnis Slough, Cook County, 1940–1947; Spring Lake Division, Upper Mississippi Wildlife and Fish Refuge, Carroll County, 1946–1948; and Calhoun Division, Mark Twain National Wildlife Refuge, Jersey County, 1947–1948.

George Arthur, Illinois Department of Conservation, banded waterfowl at the Union County Wildlife Management

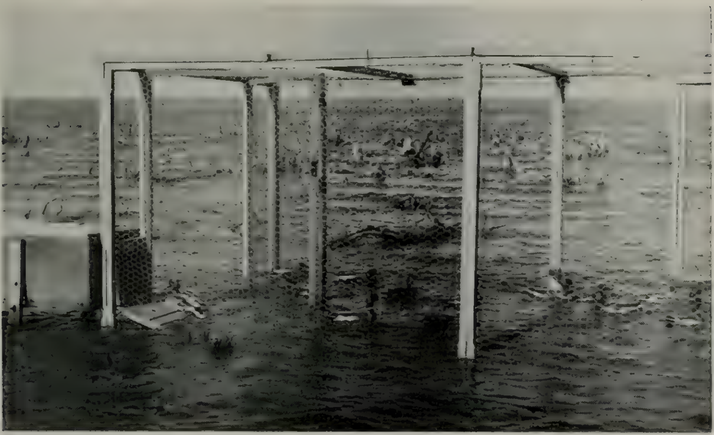

Fig. 1. — Banding trap used by personnel of the Illinois Natural History Survey to capture mallards and black ducks in shallow lakes and marshes.

Area, near Ware, Illinois, 1954–1966. Only indirect recoveries from mallards he banded in the 1954–1965 period are used in this report.

Fig. 2 shows the locations of these banding stations in Illinois.

Handling of Records

At the time of banding, ducks were classified as to species, sex, and, when possible, as to whether immature or adult. Data were recorded on our own field forms, and transferred to federal banding schedule forms in our office. The completed schedules were forwarded to the Bird Banding Laboratory at the Patuxent Wildlife Research Center, Laurel, Maryland, a branch of the Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service.

The Bird Banding Laboratory reported each recovery of a banded bird on a 3- by 4-inch file card until 1949 when the form was changed to a "flimsy," a carbon copy of band-recovery report Form 3-624. The flimsy was revised and enlarged in 1954, and in 1961 the Bird Banding Laboratory switched to IBM cards to inform both the bander and reporter of each band recovery.

We hand tabulated data from the file cards, the flimsies, and listings of our own punched IBM cards up to 1952. Band recovery data for the 1955–1966 period for all stations were tabulated by computer at the University of Illinois.

It should be noted that frequently this report uses one set of dates for bandings and another set of dates for recoveries, because indirect recoveries occur in years following the bandings. Also, in some tabulations data were omitted for certain years when band recoveries were insufficient for analysis.

Terminology

Particular definitions have been given to certain terms by the Bird Banding Laboratory. These terms are used frequently by bird banders and are essential to understanding this text. We have slightly modified the definition of most terms, as listed below, to meet the specific needs of this study.

Adults: Ducks one year of age or older.

Immatures: Young ducks fully cap-

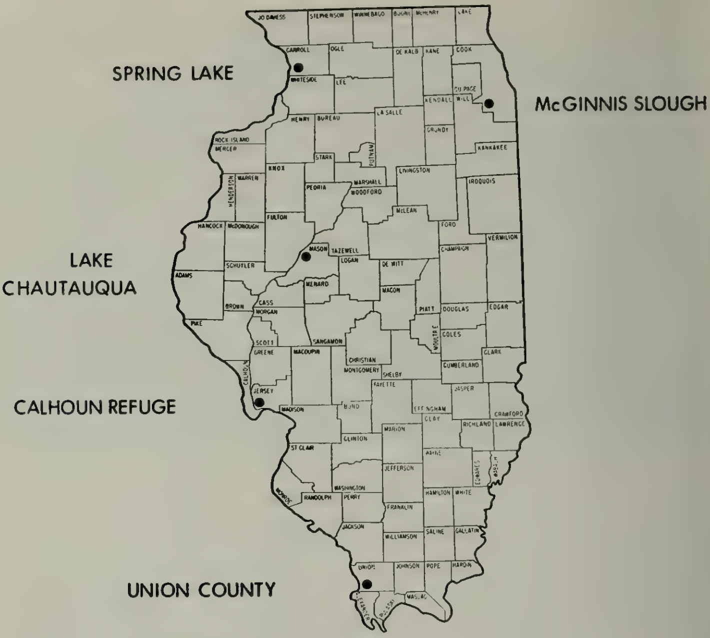

Fig. 2.—Locations of banding stations in Illinois.

able of flight but known to have hatched in the year of banding.

Recovery: A report of a banded duck killed or found dead. Over 95 percent of recoveries reported herein resulted from ducks shot by hunters. Trappers of muskrats were probably next in reporting largest numbers of banded ducks.

Direct recovery: A band recovered during the same autumn and/or hunting season as banded.

Indirect recovery: A band recovered in hunting seasons subsequent to the first.

Repeat or retrapped: The recapture of a duck within 90 days at the same trap and/or banding station where it was initially banded.

Return: The recapture of a duck at the same banding station over 90 days (usually the following fall) following initial banding.

Banding year: Our banding year started September 1 in one calendar year and ended January 15 in the next calendar year. For all practical purposes it was the hunting season in the United States and Canada, which has varied as to opening and closing dates. The closing dates in the southern zone of the United States have invariably occurred in January of the calendar year after banding but during the same banding year.

Coordinates: The latitude and longitude of a particular banding station or band recovery. A band recovery is now recorded on an IBM card by coordinates read from maps marked off in 10-minute grids.

Tabulation of Band Recoveries

At the time we first began to tabulate band recovery data in 1950, they were reported by a political or geographic designation, such as a town, county, or lake. In recording several thousand band recoveries by political designation, we found it nearly impossible to make definitive comparisons among banding stations and among years. Therefore, for species and for banding stations where large numbers of recoveries made comparisons difficult, we tabulated band recovery data by coordinates. As far as we know, this was the first use of coordinates rather than political divisions to facilitate the analysis of recovery data. Band recovery data were grouped for every 30 minutes of latitude and longitude.

IBM cards record recoveries by each degree of latitude and longitude. In both hand and computer analysis of recovery data by coordinates, degree blocks are used. For each degree of latitude, the mean of the longitudinal distribution of recoveries is determined. The mean points in each degree of latitude are connected with a line which we term an axial line. This designates the mean of the east-west distribution of recoveries within the Mississippi Flyway. The standard deviation indicates the scatter of band recoveries to the east and to the west of the mean. About two-thirds of the recoveries occur within one standard deviation of the mean. Thus, connecting the standard deviation points between each degree of latitude forms a definable geographic area, which can be depicted on a map, and can be compared with band data from other similar areas.

Our interpretation of the Mississippi Flyway (the area within the heavy lines in Fig. 3) is slightly different from that illustrated by Lincoln (1935:6). Our western border of the flyway extends from Saskatchewan to the Missouri River in central North Dakota. Then it proceeds through the middle of South Dakota and into Nebraska slightly west of the Missouri River (usually one tier of counties) to Kansas City, Missouri. It extends along county borders from Kansas City to Galveston Bay, Texas. The eastern border of the Mississippi Flyway follows state borders, the east side of Ohio, Kentucky, Tennessee, and Alabama. The relatively few band recoveries outside the flyway were not included in the analysis of recoveries by coordinates.

Throughout this study, the proportion of direct or indirect recoveries in any longitudinal-latitudinal area is equated to time. We believe there is a close relationship between the proportion of band recoveries in any geographic area (of the region delineated in this study) and the amount of time spent there by ducks during the hunting season. Thus, if indirect recoveries for a particular area amounted to 10 percent of the total recovered during a season, then we interpret this as indicating that that group of ducks spent 10 percent of the hunting season there.

RESULTS

MALLARD

Lake Chautauqua Bandings

(Our main banding effort was at the Lake Chautauqua Refuge containing a 3,700-acre shallow-basined body of water adjacent to the Illinois River. There are numerous private waterfowl clubs in the immediate area, and the most important waterfowl hunting grounds in the Illinois River valley are in an area from 10 to 20 miles downstream (southwest) from the refuge. Mallard populations on the refuge during the period of banding varied from a peak of 1,500,000 in 1944 to a low of 60,000 in 1964. Only a small number of mallards were banded prior to mid-October or after the end of November.)

Band recoveries outside of our defined limits of the Mississippi Flyway were relatively few. Fig. 3 shows all recoveries outside the defined area that resulted from banding 46,070 mallards in the periods 1939–1944 and 1947–1952 at

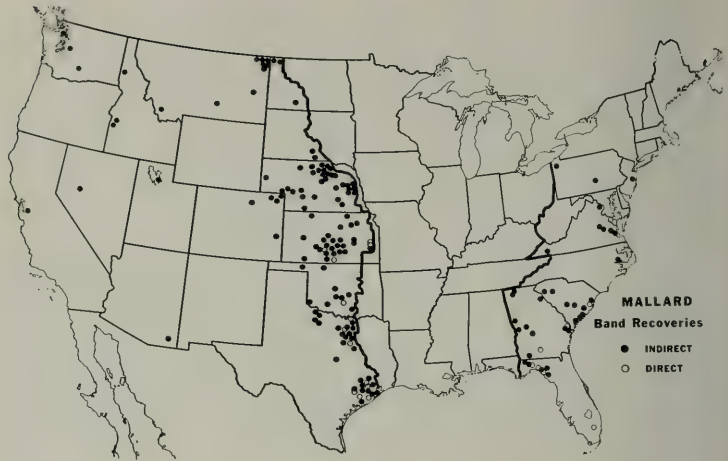

Fig. 3. — Direct and indirect band recoveries outside our defined limits (heavy lines) of the Mississippi Flyway from mallards trapped and banded at Lake Chautauqua, 1939–1944, 1947–1952.

Lake Chautauqua. Of the 5,408 indirect recoveries tabulated geographically from these bandings, 97.1 percent occurred within our defined limits of the flyway, 2.3 percent occurred west of the flyway and 0.6 percent east of the flyway. There were 2,713 direct recoveries tabulated geographically of which only 0.55 percent occurred west of the flyway and 0.29 percent east of the flyway.

Most of the mallard recoveries west of the Mississippi Flyway were in the Great Plains immediately west of the flyway border; only 12 were in the Far West. Recoveries of Illinois banded mallards in the Atlantic Flyway represented birds which were probably trapped as they were crossing the Mississippi Flyway on their way to wintering grounds in South Carolina, Georgia, and Florida. An average of 113,000 mallards wintered in South Carolina, 1960–1966; 5,000 wintered in Georgia; and 3,700 in Florida, and, of necessity, almost all of these ducks migrated through the Midwest to reach their destinations in these states.

The indirect recovery rate west of the Mississippi Flyway was 0.24 percent for adult drake mallards banded at Lake Chautauqua. For immature drakes the indirect recovery rate was 0.42 percent, and for hens of both age classes it was 0.21 percent. This suggests that immature drake mallards banded in Illinois during their first fall of life were more likely to occur in the Central Flyway in subsequent falls than were mallards banded initially as adults. Hens were less likely than drakes to leave the confines of the flyway.

Longitudinal Distribution. — The yearly axial lines of mallard *indirect recoveries* in the flyway from Lake Chautauqua bandings are shown grouped into three periods (Fig. 4, 5, and 6). In general, the axial lines are very similar through the span of 17 years. The greatest variation in the east-west distribution of axial lines usually occurs in the latitudes where the recoveries are fewest. These are latitudes with less waterfowl habitat than other latitudes.

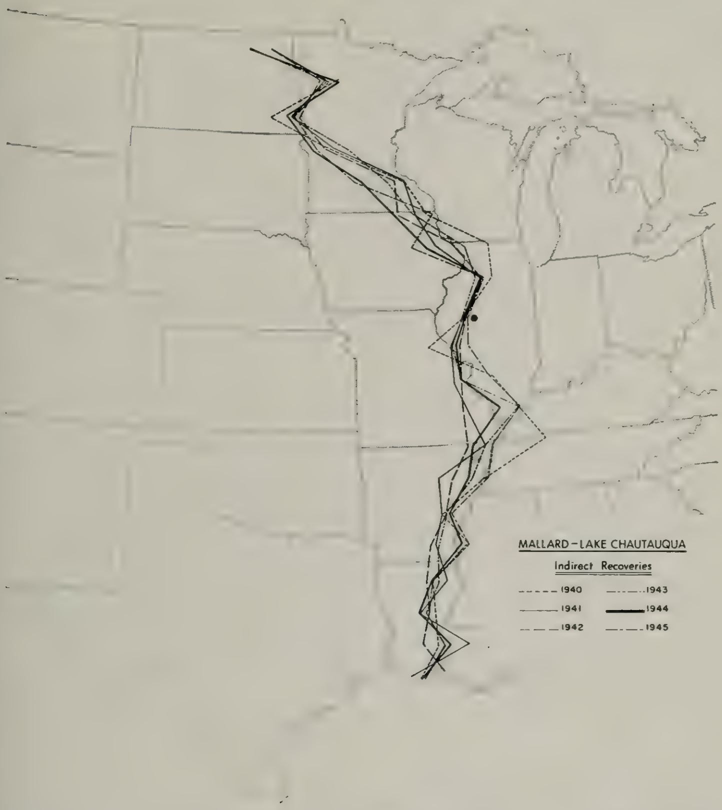

Fig. 4.—Axial lines, 1940–1945, of indirect band recoveries from mallards banded at Lake Chautauqua.

The latitude marked by the 47° and 48° parallels shows a peculiar variation in means.* In 13 of 17 years the axial lines show an abrupt swing east-southeastward, from their points of origin in northeastern North Dakota into western Minnesota, but, then, in the next zone to the south (between the 46° and 47° parallels) there is a swing back to the west, with all the mean points falling in southeastern North Dakota. This zigzag in the axial lines is apparently due to the limited distribution of mallard habitat in this zone.

It should not be inferred from the zigzag in band recoveries that the mallards shift their passage similarly. Apparently Lake Chautauqua-bound mallards pass southeastward from Saskatchewan over eastern North Dakota and western

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* For all locations of areas designated by parallels and meridians, refer to frontispiece map.

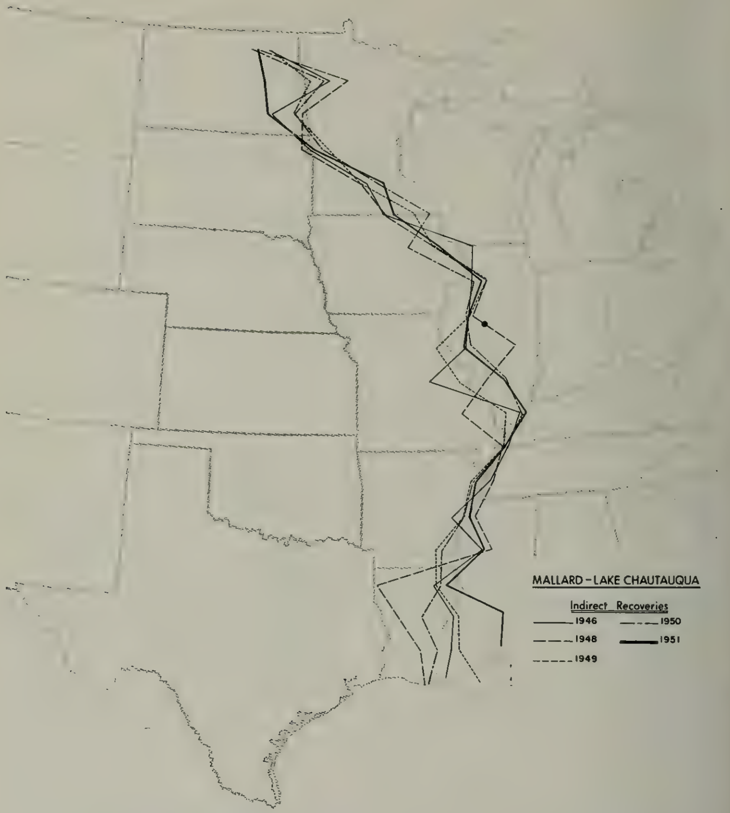

Fig. 5.—Axial lines, 1946–1951, of indirect band recoveries from mallards banded at Lake Chautauqua.

Minnesota. Many of those in the eastern elements of the migrating swarm tend to drop out in western Minnesota, whereas most of those in the western elements pass nonstop over adjacent areas in eastern North Dakota.

There is a great abundance of mallard habitat in the region of western Minnesota, and a comparative paucity of habitat in the adjacent region of east-central North Dakota. Apparently, however, in some years rains create temporary water areas on the Red River plains of North Dakota that attract elements of mallard population which previously passed nonstop; their detainment is reflected in the kill and band recoveries from the Red River Plains. Thus, particularly in 1951 and 1956, the high kill of mallards in this region of eastern North Dakota reduced the effect of the kill made in adjacent western Minnesota. The 1951 and 1956 recoveries are believed to be a more typical representation of the

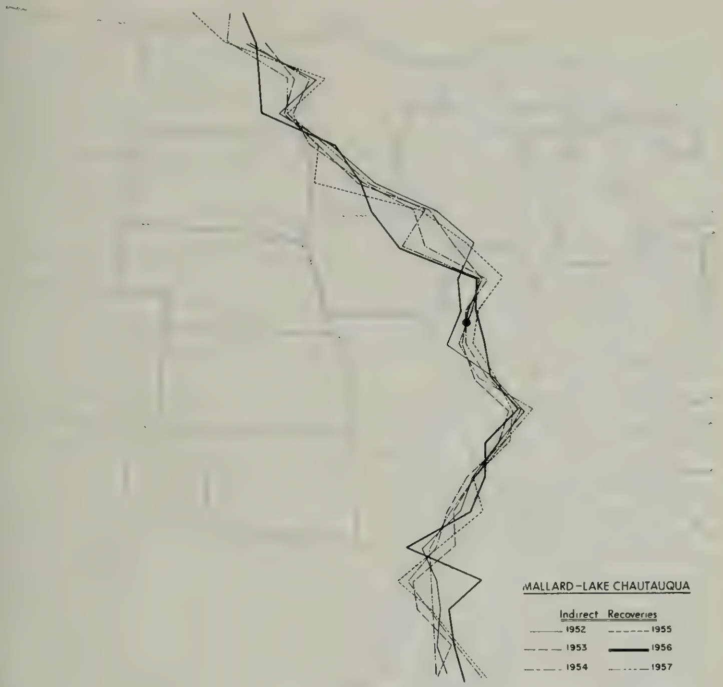

Fig. 6.—Axial lines, 1952–1957, of indirect band recoveries from mallards banded at Lake Chautauqua.

flight path taken by migrating mallards across eastern North Dakota.

In 9 of the 16 years (1940–1943, 1945, 1946, 1952, 1953, and 1955), the axial line of recoveries arrived at the Mississippi River near the border of Minnesota and Iowa. In the other 7 years (1944, 1948–1951, 1954, and 1956) the axial line arrived at the Mississippi River farther south in northwestern Illinois. We are unable to account for all of these slight shifts in axial lines in the region between the western border of Minnesota and the Mississippi River. Mass flights of ducks, largely mallards, occurred on the Upper Mississippi Wildlife and Fish Refuge during the autumns of 1940, 1946–1948, 1955, and 1956 (Green 1963:22, 24). In 3 of these 6 years (1940, 1946, 1955), the axial lines of recoveries (Fig. 4, 5, and 6) were close to the Upper Mississippi Refuge, but in 2 of the years of mass flights (1948, 1956) the axial lines fell farther west. However, by far the largest mass movements of mallards on the Upper Mississippi Refuge occurred in 1940 and 1955 (op. cit. :24), and this is reflected in the proximity of the 1940 and 1955 axial lines to the upper Mississippi River. Both the 1940 and 1955 mass migrations of mallards and other ducks were the result of unusually severe storms (Bellrose 1957:21). In our opinion, the strong northwest to west winds of these storms partially drifted large segments of Chautauqua-banded mallards east of their customary lines of flight, thereby accounting for the eastward swing in the axial lines in southern Minnesota.

There is considerable variation in the yearly east-west location of the axial lines of mallard band recoveries (Fig. 4, 5, and 6) in the lower wintering grounds. The lower wintering grounds extend south from the Arkansas River in Arkansas to the Louisiana coast. Only a small proportion of the mallards in the Mississippi migration corridor (Bellrose 1968:8) winter in this region. Consequently, the yearly shifts in east-west distribution represent only relatively small numbers of mallards. The change in location of the axial line on the lower wintering grounds for the mallard appears to be related to shifts in the availability of food. Streams flood at different times in the various watersheds, accounting for much of the shift in abundance of mallards, which are quick to move east or west to newly flooded feeding grounds.

There are two regions where the yearly axial lines are similar — in the vicinity of the banding station at Lake Chautauqua and between northern Tennessee and the Arkansas River of Arkansas. The first region emphasizes the consistent tendency each year for Lake Chautauqua mallards to return to the vicinity of their banding site. The second region emphasizes the stability of food supplies in the rice region of Arkansas where large tracts of swamp land are managed specifically for mallard hunting.

The standard deviation analysis of indirect mallard recoveries from Lake Chautauqua is shown for two periods, 1940–1954, and 1955–1959 (Fig. 7). There are only slight differences in the geographic distribution of band recoveries between these two periods, suggesting that there was no basic change in migration patterns during the two periods.

During these time periods there might have been a gradual shift in mallard populations from the Illinois to the Mississippi rivers in Illinois. Our belief was based upon relative fall populations in these two areas (Mills et al. 1966:21). But apparently the increase in mallards in the Mississippi River valley of Illinois during the 1955–1964 period over that of the 1946–1954 period (op. cit. :21) did not accrue at the expense of mallard populations customarily frequenting the Illinois River valley.

Because about two-thirds of the band recoveries occur within the lines delineating the standard deviation, these lines mark the significant limits of recoveries from the Lake Chautauqua banding station. The spread in longitudinal distribution of recoveries is greatest on the mallard breeding grounds in Saskatchewan and Manitoba, and smallest in the area of the banding station. The largest spread extends over a width of 500 miles, the smallest spread extends over a width of 70 miles, and the broad span over most of the area delineated is about 150 miles.

The distribution of individual band recoveries in Canada from mallards banded at Lake Chautauqua is given in Fig. 8. Most of these recoveries were reported by hunters and were taken during the fall. A few recoveries were obtained from fur trappers and were taken in early spring. For the most part, the recoveries were from the grassland and parkland region of southwestern Manitoba and of eastern Saskatchewan,

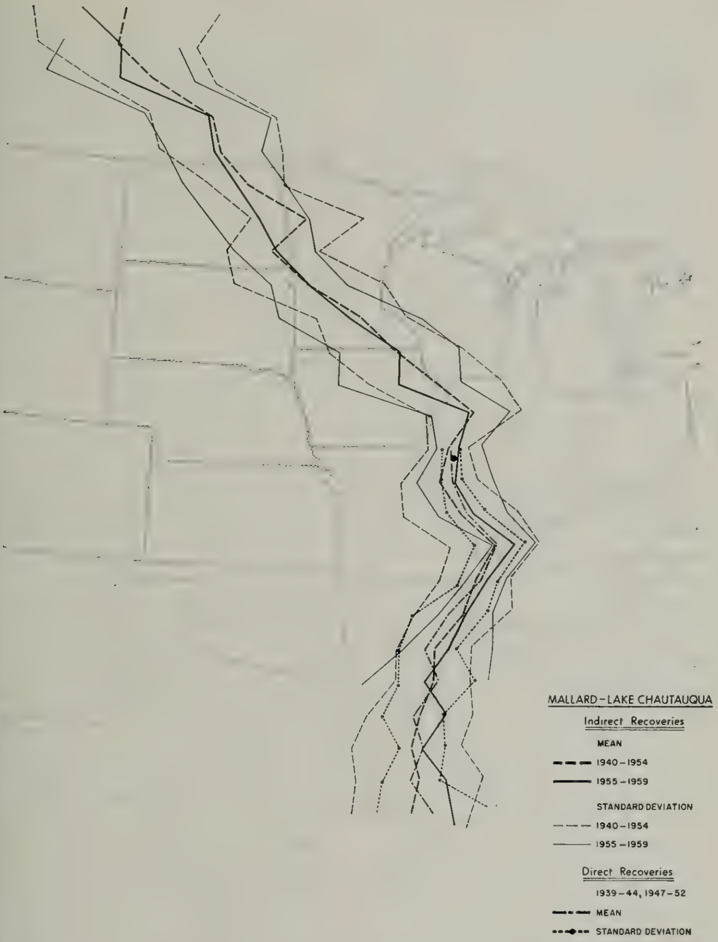

Fig. 7. — A comparison of the longitudinal distribution of indirect mallard band recoveries from Lake Chautauqua bandings for two periods, 1940–1954 and 1955–1959. The direct band recoveries for the periods 1939–1944 and 1947–1952 are also shown.

south of the Saskatchewan River.

The yearly axial lines for *direct recoveries*, 1939–1944 and 1947–1952 (Fig. 7), conform to the pattern of the indirect recovery means in the lower half of the Mississippi Flyway. However, at some latitudes there is a greater variation between years among the means of

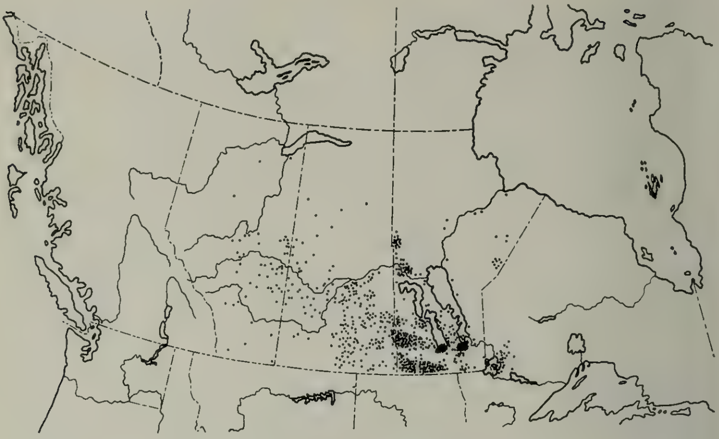

Fig. 8.—The distribution of individual indirect band recoveries in Canada, 1940–1954, from mallards banded at Lake Chautauqua.

direct as compared to those of indirect recoveries.

Yearly variation is especially evident in direct recovery means recorded between the 37° and 38° parallels. In five years (1939, 1944, 1950–1952) the axial lines fell near the mouth of the Wabash River 250 miles southeast of the banding station as a result of the unusually large number of recoveries from Hovey Lake, in the southwest corner of Indiana.

All of our information points to sizable late season departures during the fall to Hovey Lake from the Illinois River valley. Apparently in those years we banded unusually large numbers of mallards which were late migrants. Our chronology of fall-banded mallards varied from year to year depending upon trap locations, weather conditions, and availability of food.

The summary distribution of direct band recoveries, 1939–1944 and 1947–1952, by longitude mean and standard deviation is given in Fig. 7. The axial and standard deviation lines are quite similar to those for indirect recoveries in the lower half of the Mississippi Flyway. The principal difference in the distribution between direct and indirect recoveries occurs in the latitude of the banding station and the latitudes immediately to the south.

Table 1 shows the longitudinal distribution of direct and indirect mallard recoveries for the degree of latitude (40°–41°) embracing the Lake Chautauqua banding station. The means are almost identical for both direct and indirect band recoveries, being slightly to the west of the banding station, which was located within 2 miles of the 90° meridian. Both direct and indirect recoveries predominated to the southwest of the station because the more extensive hunting grounds located there biased recoveries in that direction.

The standard deviation implies that two-thirds of the recoveries occurred within an average of ±0.35 of a degree for direct recoveries and ±0.55 of a degree for indirect recoveries. Since at this latitude 1 degree of longitude equals 52.5 miles, the breadth of the standard deviation of direct recoveries was about

Table 1.—A comparison of the longitudinal distribution of direct and indirect mallard recoveries, 1939–1952, from bandings at Lake Chautauqua, Mason County, Illinois, for the degree of latitude of the banding station (40°–41°). Banding station located at about 90° longitude.[a]

	Direct Recoveries		*Indirect Recoveries*	
Year	Mean	Standard Deviation	Mean	Standard Deviation
1939	90.18	0.16	. . .	. . .
1940	90.25	0.32	90.12	0.31
1941	90.31	0.43	90.29	0.34
1942	90.17	0.38	90.30	0.32
1943	90.26	0.56	90.43	0.32
1944	90.21	0.32	90.36	0.72
1949	90.26	0.19	90.27	1.96[b]
1950	90.21	0.16	90.31	0.94
1951	90.20	0.36	90.34	0.61
1952	90.17	0.57	90.18	0.87
Average	*90.22*	*0.35*	*90.29*	*0.55*

[a] At latitude of banding station, 1 degree of longitude equals 52.5 statute miles.

[b] Omitted from average because two recoveries, one 8 degrees east of mean and the other 5.5 degrees west of mean, greatly biased standard deviation of remaining 48 recoveries.

36.7 miles and that of the indirect recoveries was about 57.7 miles. Direct recoveries represent mallards that were using Lake Chautauqua for resting and feeding, and a radius of 18.35 miles was the distance within which most mallards fed in fields and other lakes. Observations on the daily feeding flights of mallards from Lake Chautauqua confirm that most go no farther than 30 miles. Only rarely have we followed local field-feeding flocks as far as 45 miles.

The difference in longitudinal standard deviations between direct and indirect recoveries indicates that almost two-thirds of the mallards banded in previous years returned to the same longitude as Lake Chautauqua; the others that stopped at the same latitude were prone to make their migratory home in other areas, most of which were within a radius of 50 miles of Lake Chautauqua.

Latitudinal Distribution.—The longitudinal distribution of band recoveries has been appraised for Lake Chautauqua mallards by mean and standard deviation analysis. We now consider the latitudinal distribution of mallard band recoveries by comparing the proportion of band recoveries for each degree of latitude.

Table 2 shows the yearly proportion of *indirect band recoveries* for each degree of latitude between central Saskatchewan and the Gulf of Mexico, 1940–1946 and 1948–1966. In the degree of latitude including the banding station at Lake Chautauqua, the percentage of indirect recoveries varied between 10.5 and 29.3 percent.

Yearly variation in the percent of indirect mallard recoveries in the latitude of the banding station appears related first to habitat conditions and population density, and second to weather.

In the degree of latitude immediately north of the banding station, unusually large numbers of indirect recoveries were received in 1941, 1943, and 1946. Band recoveries were especially numerous along the upper Illinois River valley (1941, 1943) and the Mississippi River valley, Oquawka-Moline (1946). However, of all regions in which indirect recoveries were recorded, the largest variation from year to year occurred on the wintering grounds south of Illinois (Table 2). Eastern Arkansas north of the Arkansas River and the adjacent region of Mississippi provided most of the recoveries, amounting to 11.6 percent. In most years, there was an inverse relationship between the proportion of recoveries in the north Arkansas (35°–36°) and mid-Arkansas (34°–35°) regions. In 1950 an unusually high proportion of indirect recoveries (13.8 percent) came from the Obion River-Reelfoot Lake area of Tennessee (36°–37°).

Comparatively few indirect band recoveries came from mallards south of the Arkansas River from 1940 through 1955, except in 1940. In that year 13.8 percent of all indirect recoveries occurred in Louisiana and the adjacent

Table 2.—The number and percent of indirect band recoveries, 1940–1946 and 1948–1966,[a] for mallards banded at Lake Chautauqua, by degrees of latitude.

Degree of Latitude[b]	*1940*	*1941*	*1942*	*1943*	*1944*	*1945*	*1946*	*1948*	*1949*	*1950*	*1951*	*1952*	*1953*	*1954*	*1955*	*1956*	*1957*	*1958*	*1959*	*1960–66*	*Average*
	(166)	(428)	(557)	(519)	(693)	(601)	(218)	(128)	(297)	(515)	(495)	(587)	(698)	(388)	(311)	(261)	(280)	(169)	(99)	(232)	
56 +	0.6	0.0	0.0	0.4	0.0	0.3	0.0	0.0	0.0	0.0	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
55–56	0.0	0.7	0.0	0.4	0.2	0.0	0.0	0.8	0.0	0.4	0.0	0.0	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2
54–55	0.6	0.9	0.0	0.2	0.3	0.3	0.0	1.6	1.0	0.2	0.6	0.3	0.6	0.8	0.6	0.0	0.7	0.0	0.0	0.4	0.5
53–54	1.2	2.1	0.9	0.0	1.0	0.8	1.4	1.6	3.0	1.7	2.6	0.3	2.0	2.8	1.0	0.8	0.7	1.2	3.0	0.4	1.4
52–53	0.6	1.7	0.7	0.6	1.2	0.2	0.9	0.8	2.4	1.6	1.0	1.2	1.2	2.6	1.6	1.5	0.4	0.6	3.0	1.7	1.3
51–52	2.5	1.4	2.2	1.0	1.9	0.5	1.8	0.8	2.4	1.6	1.0	1.5	3.3	2.8	4.8	3.8	3.9	1.8	5.1	4.3	2.4
50–51	2.5	1.9	2.7	2.7	2.5	2.2	6.0	4.7	6.7	3.9	5.9	6.0	7.8	6.2	5.5	6.2	3.2	5.9	2.0	5.2	4.5
49–50	3.6	2.4	2.0	1.7	1.3	3.3	3.7	3.1	4.4	3.5	2.0	2.6	2.8	4.9	2.9	2.7	3.9	2.4	2.0	5.2	3.0
48–49	0.0	5.4	3.6	3.1	2.6	5.3	4.2	7.0	5.7	4.6	4.0	5.6	3.3	4.4	1.6	4.2	1.1	1.8	1.0	3.4	2.9
47–48	4.2	3.7	0.9	2.9	2.3	1.7	3.2	5.5	2.4	2.7	3.0	1.9	3.9	2.1	1.0	5.7	2.9	1.2	3.0	3.0	2.9
46–47	3.6	3.1	2.5	3.9	5.8	5.0	1.8	4.7	7.7	5.6	4.5	4.1	5.3	2.3	2.9	1.5	2.9	2.4	3.0	1.7	3.7
45–46	4.8	4.9	6.3	7.1	7.8	4.7	6.4	3.9	7.4	6.0	3.6	4.4	5.6	2.1	2.9	2.7	1.1	1.8	4.0	4.3	4.6
44–45	5.4	3.7	6.5	5.8	4.0	6.0	6.9	2.3	5.4	5.0	5.7	5.4	5.8	4.6	1.3	3.4	1.4	3.5	0.0	7.8	4.5
43–44	3.6	4.4	3.6	3.1	3.9	2.8	2.8	1.6	3.7	2.7	3.2	3.6	2.7	3.3	1.9	2.7	1.8	3.0	10.1	4.3	3.4
42–43	4.2	1.9	1.6	2.5	1.2	1.5	5.5	0.0	2.0	0.6	2.8	2.9	1.4	1.8	2.3	1.1	3.6	3.0	4.0	3.0	2.3
41–42	9.0	14.0	8.6	14.8	6.6	6.5	11.0	6.2	5.7	3.3	4.8	5.3	7.5	7.5	8.7	5.7	7.5	7.7	9.1	9.1	7.9
40–41[d]	19.3	20.6	19.0	16.2	21.6	21.1	15.6	12.5	16.8	10.5	19.0	25.0	16.1	19.3	27.4	18.9	29.3	19.4	21.3	23.3	19.6
39–40	5.4	6.5	9.3	5.0	4.8	2.5	4.1	2.3	3.0	4.7	8.7	5.8	8.1	9.0	7.1	6.5	5.3	2.4	5.1	3.9	5.5
38–39	1.2	2.3	2.7	2.1	1.4	2.0	1.4	1.6	0.3	2.5	2.6	1.9	1.7	2.8	2.6	5.0	6.1	8.9	2.0	3.5	2.7
37–38	0.0	0.2	1.8	1.9	3.0	3.0	1.8	3.9	1.7	4.1	4.5	5.6	3.1	3.1	6.7	3.1	6.1	11.1	7.1	3.0	3.7
36–37	1.2	0.9	3.1	2.5	3.6	4.3	0.9	5.5	6.1	13.8	8.1	3.1	4.2	4.9	5.1	4.2	9.3	8.9	5.1	3.0	4.9
35–36	2.5	8.4	5.4	2.7	4.6	6.5	6.4	11.7	3.4	10.0	4.3	3.4	4.1	3.6	4.5	8.8	4.6	5.3	3.0	3.0	5.3
34–35	7.2	1.2	9.0	7.7	9.8	9.8	8.7	10.1	3.7	4.4	5.1	4.3	2.8	3.3	4.8	6.9	2.1	5.3	7.1	3.0	5.8
33–34	3.0	1.7	0.9	1.0	2.8	3.5	0.9	2.3	1.0	2.9	0.4	1.0	1.2	2.1	0.0	1.1	1.4	1.8	0.0	0.9	1.5
32–33	1.2	2.8	1.4	4.4	2.0	1.5	0.9	1.6	1.0	0.8	0.8	0.7	0.5	0.5	0.3	0.8	0.0	0.6	0.0	0.4	1.1
31–32	3.6	0.9	2.3	2.7	1.2	1.2	1.4	0.0	0.7	0.4	0.4	0.2	0.9	0.3	0.6	0.8	0.0	0.0	0.0	0.0	0.9
30–31	4.2	1.4	1.8	1.3	1.4	1.5	1.8	1.6	1.7	0.8	0.2	1.2	0.9	1.3	1.6	1.1	0.0	0.0	0.0	0.9	1.2
29–30	4.8	0.9	1.2	2.3	1.2	2.0	0.5	2.3	0.7	1.6	0.4	2.7	2.3	1.3	0.3	0.8	0.7	0.0	0.0	1.3	1.4
Total	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*99.2*

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[a] 1947 omitted because band recoveries were insufficient for analysis.
[b] Percent determined for the midpoint between each of the two latitudes listed.
[c] Figures in parentheses represent the number of indirect recoveries analyzed by latitude.
[d] Lake Chautauqua.

region of Mississippi. This extreme proportion from the Deep South probably resulted from the worst fall storm in history, which struck the Midwest on November 11, forcing hundreds of thousands of mallards south ahead of their customary migration time.

Surprisingly, only 1.7 percent of all indirect recoveries occurred on the 3,500,000-acre coastal marsh of Louisiana. Most of the other species of dabbling ducks in the Mississippi Flyway winter on this coastal marsh, but it is apparent that wintering Illinois-banded mallards predominated in the swamp lands to the north of the coastal marshes.

The latitudinal distribution of *direct band recoveries* for mallards banded at Lake Chautauqua is shown in Table 3. The latitudes shown extend from 1 degree north (41°–42°) of the banding station (40°–41°) to the Gulf of Mexico. The yearly variation in the proportion of direct recoveries in the vicinity of the banding station varied from a low of 33 percent in 1939 to a high of 68.2 percent in 1951.

The principal reason for the yearly variation for direct recoveries in the vicinity of the banding station was variation in the chronology of banding. In those years when the proportion recovered was lowest (1939, 1941, 1942, 1943, 1944), bandings tended to be late in the fall; when the proportion recovered was highest (1940, 1949, 1950, 1951, 1952) the bandings tended to be early in the fall. Food, water, and weather conditions were other factors which influenced the yearly rate of direct recoveries near the banding station.

The percentages of direct and indirect recoveries, distributed among the latitudes from 1 degree above the Lake Chautauqua banding station to the Gulf of Mexico, are compared in Table 4. Between the 40° and 41° parallels, the location of the banding station, direct recoveries were about 1.7 times greater than indirect recoveries. However, upon considering only the 1 degree of latitude immediately above, and the 1 degree below the banding station, we find that the indirect recoveries were greater than direct recoveries. This suggests that some of the Lake Chautauqua mallards dropped out of migration immediately prior to reaching their migratory home destination of Chautauqua and that some slightly overshot their destination. In

Table 3. — The percent of direct band recoveries, 1939–1944 and 1949–1952, for mallards banded at Lake Chautauqua, by degrees of latitude.

Degree of Latitude	*1939*	*1940*	*1941*	*1942*	*1943*	*1944*	*1949*	*1950*	*1951*	*1952*	*Average*
	(100)[a]	(386)	(116)	(432)	(340)	(206)	(187)	(177)	(383)	(266)	
41–42	2.0	8.8	13.8	5.1	10.6	3.9	4.3	0.6	4.4	4.9	6.1
40–41[b]	33.0	63.7	47.4	42.8	44.1	47.1	53.5	59.9	68.2	60.1	53.7
39–40	9.0	6.0	14.6	4.9	7.0	7.3	5.9	9.6	8.9	12.8	7.9
38–39	3.0	3.6	5.2	6.5	2.6	1.9	2.7	2.3	2.9	3.4	3.6
37–38	1.0	0.8	0.9	2.8	1.5	2.9	4.8	7.3	4.4	3.4	2.9
36–37	9.0	0.8	1.7	6.0	1.8	7.3	11.8	12.4	3.7	3.7	5.0
35–36	8.0	3.1	1.7	13.9	6.2	9.2	9.1	5.7	3.9	3.7	6.7
34–35	11.0	6.2	5.2	8.3	10.6	12.6	5.9	1.1	3.1	4.9	6.8
33–34	3.0	2.1	2.6	1.1	1.8	1.9	0.0	0.0	0.5	0.0	1.2
32–33	7.0	1.8	3.4	1.4	5.3	1.5	1.0	0.0	0.0	0.8	1.9
31–32	6.0	1.0	0.9	2.3	3.2	0.5	0.0	0.0	0.0	0.4	1.3
30–31	6.0	1.3	1.7	1.9	3.8	2.4	0.5	1.1	0.0	0.4	1.7
29–30	2.0	0.8	0.9	3.0	1.5	1.5	0.5	0.0	0.0	1.5	1.2
Total	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*

[a] Figures in parentheses represent number of recoveries.

[b] Lake Chautauqua.

Table 4. — A comparison of the latitudinal distribution of direct and indirect recoveries of mallards from 1 degree north of the banding station at Lake Chautauqua to the Gulf of Mexico for the years 1939–1952.

Degree of Latitude	*Percent of Recoveries*	
	Direct	Indirect
41–42	6.1	12.8
40–41 [a]	53.7	30.8
39–40	7.9	9.9
38–39	3.6	3.3
37–38	2.9	4.7
36–37	5.0	8.0
35–36	6.7	8.4
34–35	6.8	9.9
33–34	1.2	2.6
32–33	1.9	2.8
31–32	1.3	2.0
30–31	1.7	2.2
29–30	1.2	2.6
Total	*100.0*	*100.0*

[a] Lake Chautauqua.

the zone embracing all 3 degrees of latitude including the banding station, direct recoveries were 1.3 times greater than indirect recoveries.

The implication from this comparison of direct and indirect recoveries is that about 60 percent of the mallards from bandings in previous years returned to within a 60-mile north-south zone centering on the banding station. About 80 percent of the mallards from previous bandings returned to areas within a 200-mile north-south zone centering on the banding station. These areas were primarily in the vicinity of the banding station, secondarily on the upper Illinois River above Peoria, and lastly on the lower Illinois River below Browning. Hence, about 20 percent of previously banded mallards appeared to have overflown the Illinois River valley, many continuing directly south to their principal wintering grounds.

Year in and year out, the principal wintering grounds for the mallards in the Mississippi Flyway lie between the 37° parallel and the Gulf of Mexico. Within this region, the greatest concentration of wintering mallards occurs in eastern Arkansas between the 34° and 36° parallels.

Direct recoveries south of the 37° parallel amounted to 25.8 percent while indirect recoveries amounted to 38.5 percent, almost 13 percent greater. Thus, of the 20 percent greater indirect than direct recoveries south of the banding station, 13 percent occurred on the wintering grounds. Direct recoveries on the wintering grounds were 1.5 times more frequent than indirect recoveries.

Direct recoveries indicate that there is some *reverse migration* — that each autumn some mallards move back north varying distances from the Chautauqua banding station. The longitudinal mean of these recoveries approximates the mean of indirect recoveries.

The distribution of direct recoveries by degrees of latitude north of the banding station is presented in Table 5. Of the 7.59 percent of the direct recoveries occurring north of Lake Chautauqua, 5.95 percent were within 1 degree of latitude (69 statute miles). Only three recoveries from reversed movements occurred north of South Dakota. These recoveries probably represent ducks which overshot their migratory home areas and were trapped prior to reorientation northward.

Table 5.— The latitudinal distribution of direct recoveries, 1939–1944 and 1947–1952, from mallards banded at Lake Chautauqua (40°–41°).

Degree of Latitude	*Recoveries*	
	Number	Percent
48–49	1	0.04
47–48	1	0.04
46–47	1	0.04
45–46	6	0.23
44–45	7	0.27
43–44	12	0.45
42–43	15	0.57
41–42	157	5.95
29–41 [a]	2,436	92.41
Total	*2,636*	*100.0*

[a] Recoveries from south of Lake Chautauqua.

McGinnis Slough Bandings

(McGinnis Slough is a body of water of only 300 acres situated in the southwestern part of Cook County, Illinois. It is rather isolated from other waterfowl habitat. The nearest important waterfowl hunting habitat lies on the upper Illinois River, especially from Channahon to Bureau, some 20 to 85 miles west and slightly south of McGinnis Slough. Additional small acreage of waterfowl habitat occurs in northwestern Indiana.)

Longitudinal Distribution. — A summary of *indirect band recoveries* for mallards by longitude, 1941–1951, is shown in Fig. 9. The axial and standard deviation lines show a longitudinal distribution down the flyway almost identical to that for bandings of mallards at Lake Chautauqua. The only important differences between the two stations occur between 40° and 45° of latitude, where the axial and standard deviation lines are farther east for McGinnis Slough recoveries. The slightly greater eastward swing for McGinnis Slough mallards begins in southern Minnesota and ends on the Mississippi River in west-central Illinois.

North of the McGinnis Slough banding station in the United States, the spread of band recoveries varied from a maximum of 350 miles to a minimum of 100 miles and averaged about 225 miles. South of the banding station, spread in band recoveries varied from a maximum of 270 miles to a minimum of 120 miles with an average of about 170 miles.

The standard deviation in the longitudinal distribution of band recoveries at the latitude of the McGinnis Slough banding station was 200 miles. This is more than twice the spread for indirect recoveries of Lake Chautauqua banded mallards in the vicinity of their station. The difference arises from the small size of McGinnis Slough, the paucity of hunting in its immediate vicinity, and the importance of the upper Illinois River valley for mallard hunting, some 20–85 miles to the west.

Table 6 shows the yearly variation in the mean longitude and standard deviation for indirect band recoveries occurring at the latitude of the McGinnis Slough banding station. The mean varied from 0.12 to 1.47 degrees west of the banding station during the 9-year period. The standard deviation displayed a considerable yearly variation; some years those mallards returning to the latitude of McGinnis Slough were widely dispersed, east and west, and other years they were well grouped near the station. But in general, there is evidence of a

Table 6. — Indirect mallard band recoveries, 1943–1951, by mean degree of longitude[a] and its standard deviation for the degree of latitude (41°–42°) at which the ducks were banded at McGinnis Slough, Cook County, Illinois. Station located at about 87.9° longitude.

Year	*Number of Recoveries*	*Mean Degree of Longitude*	*Degrees from Station*[b]	*Standard Deviation in Degrees*
1943	12	89.33	+1.47	2.11
1944	48	88.35	+0.79	5.10
1945	43	88.51	+0.65	1.37
1946	36	88.90	+1.04	1.57
1947	34	88.08	+0.12	0.62
1948	9	89.19	+1.33	4.75
1949	20	89.23	+1.37	0.51
1950	13	88.29	+0.43	0.32
1951	9	89.08	+1.22	0.78
Average		*88.77*	*+0.91*	

[a] 1 degree of longitude at this latitude equals about 52 statute miles.
[b] —Denotes degrees east of station, + denotes degrees west of station.

strong homing tendency for McGinnis Slough mallards. Considering the small size of McGinnis Slough and its out-of-the-way location for mallards, it is a remarkable display of return.

The longitudinal distribution of mallard *direct recoveries,* 1940–1947, for McGinnis Slough bandings, along with the distribution of indirect recoveries is shown in Fig. 9. The axial line of direct recoveries occurs from 10 to 50 miles east of that for the indirect recoveries

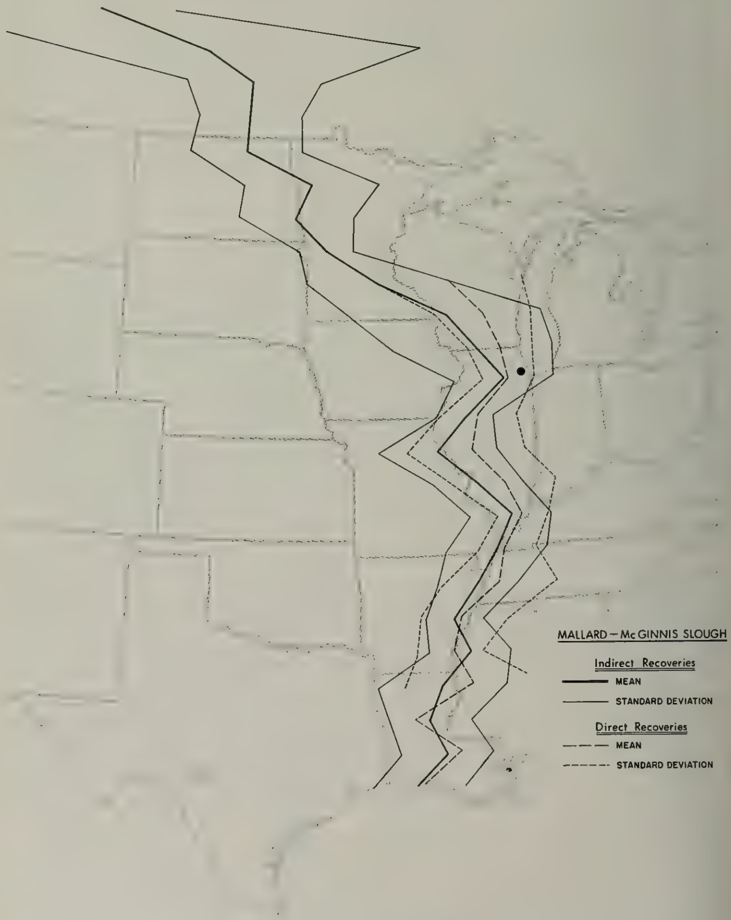

Fig. 9. — The longitudinal distribution of mallard indirect recoveries as compared with direct recoveries on the basis of mean and standard deviation lines. Mallards banded at McGinnis Slough, Cook County, Illinois, 1940–1947.

between the banding station and the main wintering grounds near Stuttgart, Arkansas. North of the banding station, the direct mallard recoveries, representing a reversed movement, tend to occur in central Wisconsin, about 50 miles to the east of the line for most indirect recoveries.

The axial line and standard deviation for the direct recoveries represent the migration corridor used by McGinnis Slough mallards between that area and the wintering grounds. The slight westward distribution of the indirect recoveries is more in keeping with the mass mallard passage through Illinois to the wintering grounds. It is evident that some mallards banded at McGinnis Slough are "captured" by other mallard population elements passing in subsequent years to the west of McGinnis Slough.

Latitudinal Distribution. — The latitudinal distribution of *indirect recoveries* for mallards banded at McGinnis Slough, 1941–1951, is given in Table 7. The percentages of recoveries by latitude are similar to those of mallards banded at Lake Chautauqua except for the difference stemming from the location of the two stations. At the latitude of McGinnis Slough (41°–42°) indirect recoveries for that station amounted to 16.8 percent. On the other hand, at this latitude for Lake Chautauqua bandings, recoveries amounted to only 7.9 percent (Table 2). And at the latitude of Lake Chautauqua, recoveries from McGinnis Slough bandings amounted to only 5.4 percent. Thus, there is evidence that each banded group of mallards tended to return to the latitude where previously banded.

Table 7. — The number and percent of indirect recoveries, 1941–1951, from mallards banded at McGinnis Slough, Cook County, by degrees of latitude. Station located at about 87.9° longitude.

Degree of Latitude	*Recoveries*	
	Number	Percent
56 +	3	0.2
55–56	0	0.0
54–55	9	0.6
53–54	16	1.1
52–53	11	0.7
51–52	11	0.7
50–51	50	3.6
49–50	38	2.7
48–49	42	2.9
47–48	39	2.7
46–47	79	5.6
45–46	99	7.0
44–45	114	8.0
43–44	79	5.6
42–43	55	3.9
41–42[a]	237	16.8
40–41	77	5.4
39–40	51	3.6
38–39	28	2.0
37–38	35	2.5
36–37	70	4.9
35–36	68	4.8
34–35	89	6.3
33–34	37	2.6
32–33	17	1.2
31–32	18	1.3
30–31	24	1.7
29–30	23	1.6
Total	*1,419*	*100.0*

[a] McGinnis Slough.

Considering *direct recoveries*, mallards banded at McGinnis Slough have a recovery of 55.5 percent within the degree of latitude of the banding station (Table 8). This is close to the 53.7 percent recorded for direct recoveries from Lake Chautauqua bandings and reported near that station (Table 3). The distribution of direct recoveries from McGinnis Slough shows only a 9.7 percent recovery in the latitude of the Lake Chautauqua station. The distribution of direct recoveries on the principal wintering grounds of the mallard (34°–37°) is similar to that from bandings at Lake Chautauqua.

A comparison of direct and indirect recoveries from mallards banded at McGinnis Slough (recorded only for those degrees of latitude from 1 degree north of the banding station to the Gulf of Mexico) is given in Table 8. The important latitude for comparison is that of the banding station (41°–42°). Note

Table 8. — A comparison of the distribution of direct and indirect recoveries for the same latitudes from north of the banding station at McGinnis Slough to the Gulf of Mexico, 1941–1947.

Degree of Latitude	*Direct Recoveries*		*Indirect Recoveries*	
	Number	Percent	Number	Percent
42–43	48	6.7	40	6.0
41–42[a]	400	55.5	194	29.4
40–41	70	9.7	66	10.0
39–40	25	3.5	39	5.9
38–39	25	3.5	23	3.5
37–38	21	2.9	23	3.5
36–37	30	4.2	50	7.6
35–36	29	4.0	53	8.0
34–35	36	5.0	73	11.1
33–34	6	0.8	33	5.0
32–33	12	1.7	18	2.7
31–32	7	0.9	11	1.7
30–31	9	1.2	21	3.2
29–30	3	0.4	16	2.4
Total	*721*	*100.0*	*660*	*100.0*

[a] McGinnis Slough.

that the percentage for direct recoveries (55.5) is about 1.9 times greater than that for indirect recoveries (29.4) for the area of the banding station. The proportion of recoveries from the wintering grounds (29°–37°) amounts to 18.2 percent for the direct recoveries and 41.7 percent for the indirect recoveries. Thus, the proportion of indirect recoveries is about 2.3 times greater than the proportion of direct recoveries for the latitudes of the wintering grounds. The conclusion is reached that additional time on the wintering grounds accrued from overflights of McGinnis Slough and other habitats at that latitude.

Spring Lake Bandings

(Spring Lake is a shallow body of water of about 2,900 acres adjacent to the Mississippi River in Carroll County, Illinois. It is a division of the Upper Mississippi Wildlife and Fish Refuge. The banding station on this lake was about 115 miles west and 25 miles north of the one on McGinnis Slough, and 120 miles north of the Lake Chautauqua banding station. The 42nd degree of latitude passes 2 miles south of the banding station site. During the years of banding, 1946–1948, peak mallard populations on this lake varied between 15,000 and 25,000. Extensive waterfowl hunting habitat extended up and down the Mississippi River from this banding station.)

Longitudinal Distribution. — The mean and standard deviation of the longitude for each degree of latitude of all *indirect recoveries,* 1947–1952, for mallards banded at Spring Lake are shown in Fig. 10. With a few minor exceptions, the distribution of indirect recoveries is essentially the same as that for those from bandings at Lake Chautauqua and McGinnis Slough (Fig. 7 and 9). The principal exception to the general distribution pattern occurs in the latitudes adjacent to the Spring Lake banding station. There, the axial and standard deviation lines are about 100 miles west of those for McGinnis Slough, but almost identical to the lines representing the longitudinal distribution of Lake Chautauqua bandings.

Data in Table 9 show that in a 4-year period, variations in the mean longitude of indirect mallard recoveries represented distances from about 27 miles west of the station (1948) to about 23 miles east (1950). The average mean of band recoveries for the period, 1947–1950, was within 1 mile of the banding station. The standard deviation shows a rather limited dispersion longitudinally for 3 of the 4 years.

It is apparent that Spring Lake mallards, like those at the Lake Chautauqua and McGinnis Slough banding stations, were prone to return to the vicinity of the banding station in the years following their banding.

A comparison of the distribution of *direct recoveries* with indirect ones from Spring Lake bandings (Fig. 10) shows only minor differences. Standard deviation lines show that a more compact distribution of direct recoveries occurred

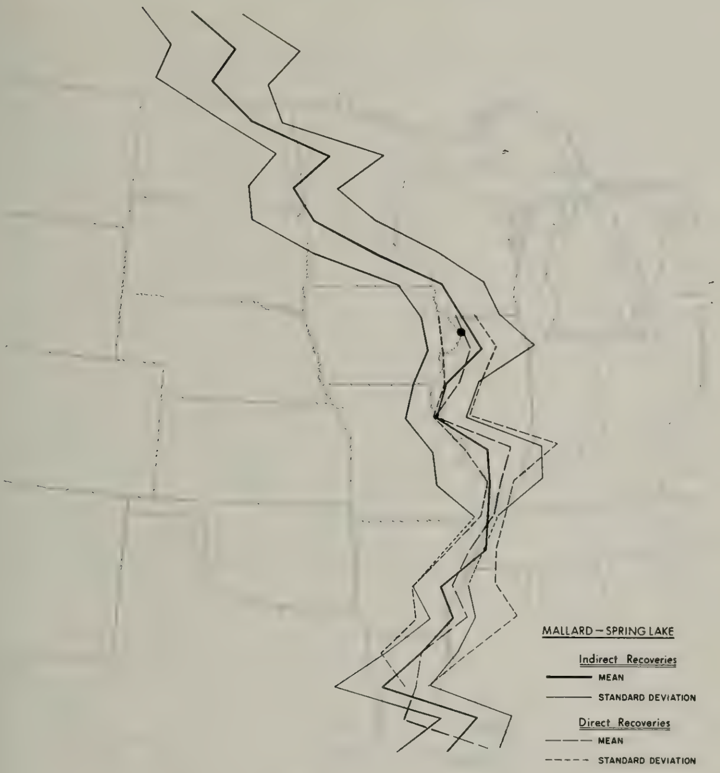

Fig. 10.—The longitudinal distribution of mallard indirect recoveries as compared with direct recoveries on the basis of mean and standard deviation lines. Mallards banded at the Spring Lake Refuge, Carroll County, Illinois, 1946–1948.

in the immediate vicinity of the banding station. South of southern Illinois there was little difference in the axial or standard deviation lines until central Louisiana, and south, a region of few recoveries.

Direct and indirect recoveries between 42° and 40° of latitude are largely from the Mississippi and Illinois River valleys, thereby accounting for the axial lines passing between these two river valleys.

The plotting of individual direct recoveries shows their distribution in the region of the Spring Lake banding sta-

Table 9.—Indirect mallard band recoveries, 1947–1950, by mean degree of longitude and its standard deviation for the degree of latitude (42°–43°) where banded at the Spring Lake, Carroll County, Illinois station. Banding station located at about 90.1° longitude.[a]

Year	*Number of Recoveries*	*Mean Degree of Longitude*	*Degrees from Station*[b]	*Standard Deviation of Recoveries*
1947	32	90.03	—0.04	1.50
1948	13	90.60	+0.53	1.75
1949	13	90.17	+0.10	2.81
1950	13	89.52	—0.45	1.91
Average		*90.08*	*+0.01*	

[a] 1 degree of longitude at this latitude equals about 51.5 statute miles.

[b] —Denotes degrees east of station, + denotes degrees west of station.

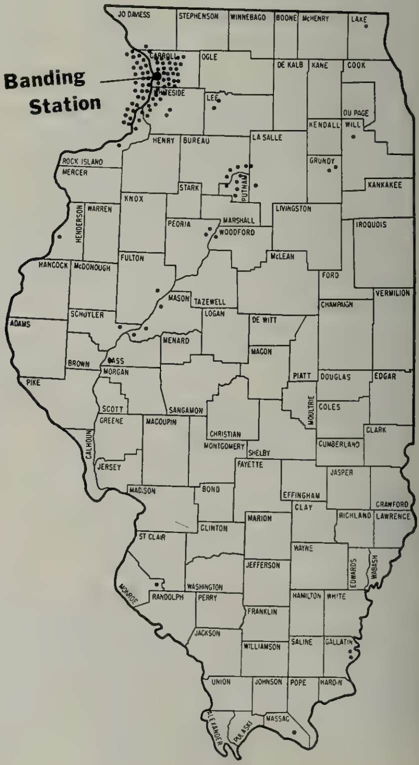

Fig. 11.—Individual direct recoveries of mallards banded at the Spring Lake Refuge, Carroll County, Illinois, during October and November, 1946.

tion (Fig. 11). Two facts are apparent — there is a cruising radius of about 25 miles around the banding station which the mallards cover in their feeding activities, and when the birds leave the area of their daily cruising range they are continuing their migratory flight. The Mississippi River valley between Muscatine, Iowa, and Alton, Illinois, supports the largest mallard concentrations in the entire Mississippi valley, yet there are few direct recoveries from this region. This indicates that mallards departing from Spring Lake in migration did not gradually move south down the Mississippi River albeit that excellent habitat was available to them. It is also evident from Fig. 11 that a sizeable contingent of Spring Lake banded mallards flew southeastward about 65 miles to the Illinois River valley near Bureau. We believe that most of these mallards had this area of the Illinois valley as their initial goal but prematurely dropped out of migratory passage at Spring Lake and were banded before continuing to their proximate goal.

Latitudinal Distribution. — The latitudinal distribution of *indirect recoveries* from mallards banded at Spring Lake is given in Table 10. Because the banding station was located only 2 miles north of the 42° parallel, approximately equal numbers of recoveries were received below and above that latitude. Therefore, at the latitude of the banding station we have combined band recoveries for 2 degrees (41°–43°) of latitude to make the data more comparable with those from other banding stations. Indirect recoveries in this delimited area amounted to 23.6 percent of the total for the flyway.

Indirect recoveries for a similar 2-degree delimited area (39°–41°) in the vicinity of the Chautauqua station (Table 2) accounted for 24.1 percent, and for McGinnis Slough (40°–42°) (Table 7) 22.1 percent, of the indirect recoveries over the entire span of migratory flight.

Table 10. — The number and percent of indirect recoveries, 1947–1952, from mallards banded at Spring Lake, Carroll County, Illinois, by degrees of latitude. Station located at about 90.1° longitude.

Degree of Latitude	*Recoveries*	
	Number	Percent
56 +	1	0.2
55–56	0	0.0
54–55	4	0.7
53–54	2	0.4
52–53	2	0.4
51–52	9	1.6
50–51	20	3.6
49–50	14	2.6
48–49	24	4.4
47–48	23	4.2
46–47	24	4.4
45–46	28	5.1
44–45	31	5.7
43–44	21	3.8
42–43 41–42 [a]	129	23.6
40–41	43	7.8
39–40	12	2.2
38–39	14	2.6
37–38	10	1.8
36–37	33	6.0
35–36	26	4.7
34–35	34	6.2
33–34	13	2.4
32–33	11	2.0
31–32	5	0.9
30–31	4	0.7
29–30	11	2.0
Total	*548*	*100.0*

[a] Data for these 2 degrees combined because banding station located so near the 42° parallel.

Direct and indirect recoveries are compared (Table 11) for similar latitudes for mallard bandings at Spring Lake. For the 2-degree area embracing the vicinity of the banding station, the percentage of direct recoveries is about 1.7 times greater than that of the indirect recoveries. However, indirect recoveries are in greater proportion than direct recoveries in the latitudes immediately north (43°–44°) and south (40°–41°) of those latitudes adjacent to the banding station. On the principal wintering grounds of the mallard (29°–37°), the relative proportion of indirect recov-

Table 11.—A comparison of the distribution of direct and indirect recoveries for the same latitudes from north of the banding station at Spring Lake to the Gulf of Mexico, 1946–1952.

Degree of Latitude	*Direct Recoveries*		*Indirect Recoveries*	
	Number	Percent	Number	Percent
43–44	2	0.6	21	5.7
42–43 41–42 [a]	189	60.9	129	35.1
40–41	22	7.1	43	11.7
39–40	6	1.9	12	3.3
38–39	5	1.6	14	3.8
37–38	11	3.5	10	2.8
36–37	20	6.4	33	9.0
35–36	16	5.1	26	7.2
34–35	18	5.8	34	9.3
33–34	5	1.6	13	3.6
32–33	7	2.3	11	3.0
31–32	5	1.6	5	1.4
30–31	3	1.0	4	1.1
29–30	2	0.6	11	3.0
Total	*311*	*100.0*	*366*	*100.0*

[a] Spring Lake.

eries is 1.5 times greater than is the proportion of direct recoveries. As at the previous stations, we believe that this difference resulted largely from overflights. About one-third of the living mallards which visited Spring Lake the year previous failed to stop and continued on in migration to their principal wintering grounds, where the additional time, accruing from the overflight, was spent.

Calhoun Wildlife Refuge Bandings

(The Calhoun National Wildlife Refuge is the southernmost division of the Mark Twain National Wildlife Refuge which encompasses federal refuge units along the Mississippi River between Rock Island and Alton, Illinois. The Calhoun division, embracing about 5,050 acres, includes several lakes adjacent to the Illinois River a few miles above its confluence with the Mississippi River at Grafton, Illinois. The banding station was located on Gilbert Lake, about 3 miles south of the 39° parallel in Jersey County. This is about 215 miles almost due south of the Spring Lake refuge. The Calhoun Refuge, at the time of our banding program, was host to peak mallard populations of 25,000–50,000. We banded only 1,500 mallards during late autumn seasons of 1947 and 1948. Direct recoveries were so few in number as to be meaningless. Indirect recoveries, 1948–1954, numbered 201 which provided data for limited analysis.)

Longitudinal Distribution.—The mean longitude for indirect recoveries for each degree of latitude shows an axial line from the breeding to the wintering grounds which is very similar (Fig. 12) to that found for indirect recoveries from the Lake Chautauqua, McGinnis Slough, and Spring Lake banding stations. At the latitude of the banding station, the axial line passed within a mile or two of the banding station. The axial line of recovery extends southeastward from Manitoba to the Mississippi River in northern Illinois, and then south to the Gulf of Mexico.

Latitudinal Distribution.—Indirect recoveries from mallards banded at the Calhoun Refuge have been analyzed by degree of recovery (Table 12). Because the banding station was located only 3 miles south of the 39° parallel, the recoveries were combined for 2 degrees of latitude, 1 degree north of the site and 1 degree south.

The 23.9 percent indirect recovery of bands from hunters within these 2 degrees of latitude is larger than the total percentage for any other 2 degrees. The largest sum for any other 2 degrees (44°–46°) is 14.9 percent. The indirect band recovery of mallards near the Calhoun Refuge banding site was almost identical to the indirect recoveries for mallards banded at the Spring Lake, McGinnis Slough, and Lake Chautauqua stations which returned to the respective latitudes of those stations.

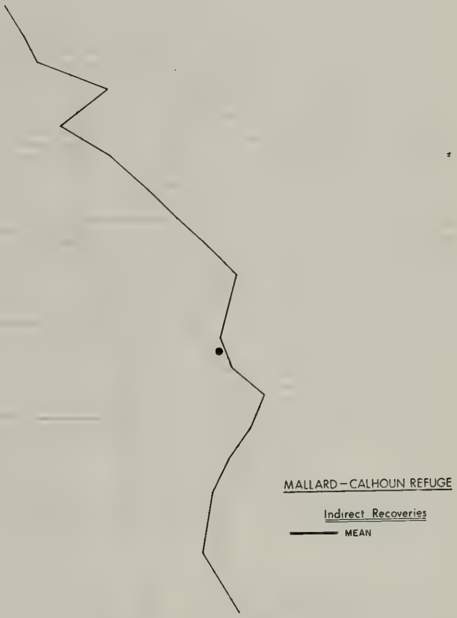

Fig. 12. — The mean line of indirect recoveries from mallards banded at the Calhoun Refuge, Jersey County, Illinois, 1947 and 1948.

Table 12.—The number and percent of indirect recoveries, 1948–1954, from mallards banded at the Calhoun Refuge, Jersey County, Illinois, by degrees of latitude. Station located at about 90.4° longitude.

Degree of Latitude	*Recoveries*	
	Number	Percent
56 +	0	0.0
55–56	0	0.0
54–55	0	0.0
53–54	2	1.0
52–53	5	2.5
51–52	3	1.5
50–51	5	2.5
49–50	6	3.0
48–49	5	2.5
47–48	5	2.5
46–47	11	5.5
45–46	14	6.9
44–45	16	8.0
43–44	11	5.5
42–43	2	1.0
41–42	2	1.0
40–41	6	3.0
39–40 38–39 [a]	48	23.9
37–38	3	1.4
36–37	14	6.9
35–36	14	6.9
34–35	12	6.0
33–34	8	4.0
32–33	0	0.0
31–32	4	2.0
30–31	2	1.0
29–30	3	1.5
Total	*201*	*100.0*

[a] Data for these 2 degrees combined because banding station located so near the 39° parallel.

Union County Bandings

(The Union County Wildlife Management Area is located 2 miles east of the Mississippi River between Ware and Reynoldsville in Union County, Illinois. This is slightly south of midway between the 37° and 38° parallels, about 320 miles south of the Spring Lake banding station, and 105 miles south of the Calhoun Refuge banding station. Mallards at this station were banded in mid- and late winter, thereby permitting only a few direct recoveries. Because of the few direct recoveries, only indirect recoveries have been analyzed for mallard bandings at this station.)

Longitudinal Distribution.—All of the indirect band recoveries from mallards banded at the Union County station which were reported during the period 1955–1966 have been analyzed by longitudinal mean and standard deviation. Fig. 13 shows that although the axial and standard deviation lines from this banding station were similar to those presented for other banding stations in Illinois, there are some slight differences.

Whereas earlier bandings at other stations showed a recovery bias originating from hunting pressure and waterfowl habitat in northwestern Minnesota, Union County mallard data do not result in this zigzag in the axial recovery line in northern United States. The path of recoveries, as delineated by standard deviation, arrived at the Mississippi River in southern Iowa slightly south of that delineated for other Illinois stations. From the Mississippi River southward, Union County recovery data are almost identical to data for all other mallard bandings in Illinois.

Table 13 shows the yearly variation in the longitudinal mean and standard deviation for indirect recoveries in the degree of latitude encompassing the banding station. The banding station was located at about 89.35° of longitude whereas the 12-year average of the mean recoveries was 88.95°, about 40 miles east of the banding location. Intensive hunting at Hovey Lake, near Mount Vernon, Indiana, resulted in this eastward pull in mean recovery location.

In 10 of the 12 years, the mean of the band recoveries fell within 55 miles east of the station. The standard deviation embraced a breadth varying from 34 miles in 1966 to 280 in 1960. Wide yearly variation in the spread in distribution is attributed to the dispersed and relatively meager waterfowl habitat available between the 37° and 38° parallels. Nonetheless, in 9 of 12 years the standard deviation indicated that two-thirds of the recoveries at the lati-

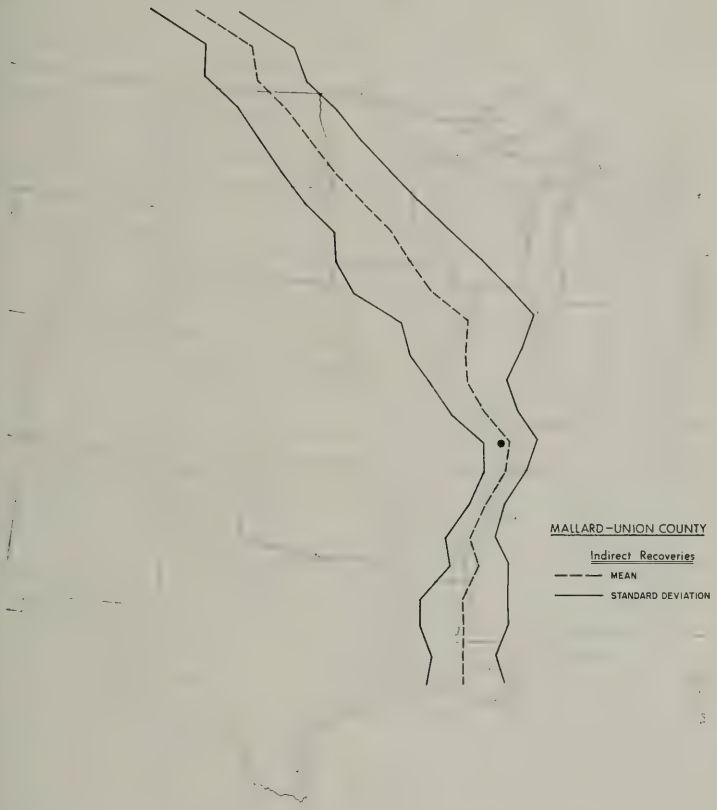

Fig. 13.—The longitudinal distribution of mallard indirect recoveries on the basis of mean and standard deviation lines. Mallards banded at the Union County Wildlife Management Area, near Ware, Illinois, 1954–1966.

tude of the banding station fell within a longitudinal span of 175 miles.

Standard deviation of indirect band recoveries from Union County is smallest from the banding station south along the Mississippi River to southern Arkansas. There the path of recoveries is only 100–140 miles wide. Standard deviation shows that the broadest recovery path is between the western border of Minnesota and the Mississippi River along the border of Illinois. In this region the delineated path is from 200 to 250 miles wide. This wide path across southwestern Minnesota and diagonally across Iowa results both from the spread in band recoveries in any one year, and from variations in the yearly mean.

Fig. 14 shows the variation in the yearly mean longitude distribution of

Table 13.—Indirect mallard band recoveries, 1955–1966, by mean degree of longitude[a] and its standard deviation for the degree of latitude (37°–38°) encompassing the Union County, Illinois, banding station. Station located at about 89.4° longitude.

Year	*Number of Recoveries*	*Mean Degree of Longitude*	*Degrees from Station*[b]	*Standard Deviation in Degrees*
1955	257	88.65	—0.70	0.75
1956	217	88.81	—0.54	1.53
1957	69	88.44	—0.91	1.15
1958	65	88.41	—0.94	1.58
1959	21	89.31	—0.04	2.38
1960	12	88.90	—0.45	2.55
1961	11	88.09	—1.26	0.75
1962	11	91.02	+2.27	5.08
1963	12	89.17	—0.18	0.54
1964	30	88.82	—0.53	1.11
1965	14	88.86	—0.49	0.52
1966	13	88.88	—0.47	0.31
Average		*88.95*		

[a] 1 degree longitude at this latitude equals about 55 statute miles.

[b] — Denotes degrees east of station, + denotes degrees west of station.

Union County mallard bandings for the recovery years, 1955–1960. For most regions of their fall passage, the band recoveries from these mallards are very similar in year-to-year distribution, but especially so along the Mississippi River from southern Illinois to southern Arkansas. The greatest divergence in the yearly axial line distribution occurred in the region between western Minnesota and the Illinois River. In this region, the 1955 axial line was farthest east and the 1957 axial line was farthest west. In 1956 the axial line of recoveries was approximately average, about midway between that of 1955 and 1957.

There were massed mallard flights each of these 3 years as described by Bellrose (1957), and Bellrose and Sieh (1960). The massed passage on November 1-2, 1955 occurred largely at night in the region between western Minnesota and the Mississippi River (Bellrose 1957:22–23). A heavy, low overcast blanketed the region and winds were strong from the west.

In contrast, the November 7, 1956 fall grand passage, through the region delineated above, occurred largely during diurnal hours (Bellrose & Sieh 1960:37–42). This migration occurred during a period when skies were overcast in the region (op. cit. 55) and winds were strong from the northwest. The great 1957 mallard passage through the region between western Minnesota and western Illinois occurred largely during the night of October 23-24 (op. cit. 53). Skies were again overcast and winds were fairly strong, but this time from the northeast.

Winds and landscape visibility may account for the divergence in the axial lines of band recoveries in 1955, 1956, and 1957 in the region from western Minnesota southeastward to the Mississippi River (Fig. 14). The 1956 grand passage is the only one of the three (1955–1957) for which band recoveries indicate that this region was crossed along customary lines of flight. The mean (Fig. 13) is based on the average of all indirect recoveries, 1955–1966. The November 7, 1956 passage occurred more extensively in daylight hours than either that of November 1-2, 1955, or October 23-24, 1957.

The 1955 axial line of recoveries between western Minnesota and the Mississippi River was from 60 to 120 miles

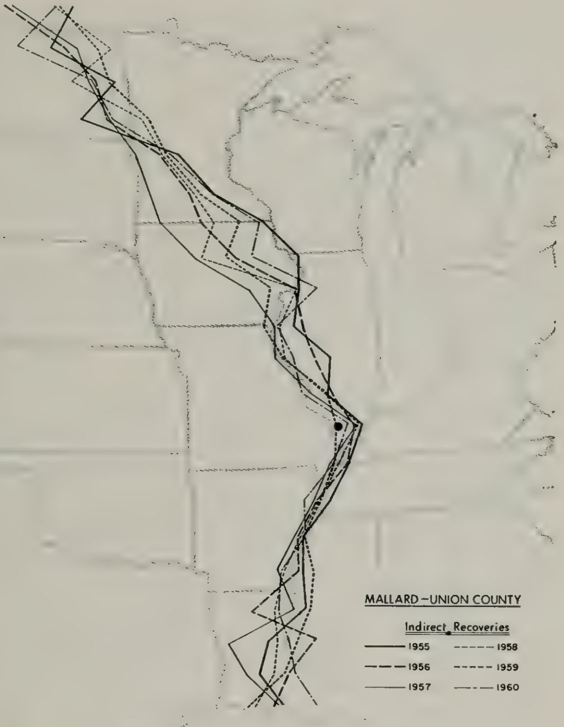

Fig. 14. — Axial lines, 1955–1960, of indirect band recoveries from mallards banded at the Union County Area, near Ware, Illinois.

east of that of 1957. In the 1955 mass flight the wind was strong from the west, while in 1957 the wind was almost as strong from the northeast. At the time of both the 1956 and 1957 mass flights, heavy, low overcast at night reduced visibility to less than a mile. The regions crossed by the passage of waterfowl in southern Minnesota and northern and eastern Iowa are devoid of salient landscape features. South of the Minnesota River, the general drainage pattern of creeks and small rivers is southeastward to the Mississippi River. When it is visible, the drainage pattern in this region provides a means of orientation. During the diurnal passage in 1956, observations made from a light aircraft by

Bellrose (Bellrose & Sieh 1960: 33, 34, 44) indicated that mallards were utilizing the larger streams of this region for navigational purposes. Nocturnal observations made by Bellrose at low altitudes from a light airplane were helpful in understanding the problems faced by migrating waterfowl at night. On nights with a low overcast, the watercourses of this region were invisible until directly below the aircraft, and woods and fields were indistinguishable. It is doubtful that on the nights of November 1-2, 1955, and October 23-24, 1957, the landscape in this region could have been used by waterfowl for prolonged orientation and/or navigation. Therefore, the variation in yearly means of longitude in the region, from western Minnesota southeastward to the Mississippi River, appears to be attributable to wind drift of migrating mallards during nights of poor visibility and strong beam winds. Landscape features were plainly visible and were used during the diurnal passage in 1956, when there was apparently no wind drift.

Latitudinal Distribution. — The latitudinal distribution of indirect mallard band recoveries from Union County is shown for the years 1955–1966 in

Table 14. — The percent of indirect mallard recoveries, 1955–1966, by latitude from bandings at the Union County banding station (37°–38°).

Degree of Latitude	*1955* (1236)[a]	*1956* (2160)	*1957* (1531)	*1958* (965)	*1959* (490)	*1960* (416)	*1961* (233)	*1962* (105)	*1963* (256)	*1964* (575)	*1965* (243)	*1966* (221)	*Average*
55–56	0.0	0.1	0.1	0.2	0.2	0.2	0.0	1.0	0.0	0.2	0.0	0.0	0.2
54–55	0.2	0.2	0.3	0.7	0.8	0.0	0.9	1.9	0.0	0.2	0.0	1.4	0.6
53–54	0.4	0.7	1.2	1.4	2.9	1.2	4.3	0.0	0.8	1.2	1.2	0.9	1.4
52–53	0.7	2.1	2.2	2.7	3.5	3.6	2.6	3.8	2.3	1.2	4.1	2.3	2.6
51–52	1.5	4.2	2.7	4.8	4.5	4.1	2.2	4.8	3.5	1.0	2.9	4.1	3.3
50–51	1.9	8.8	4.3	6.0	5.9	6.5	4.7	1.9	8.2	4.0	3.7	1.8	4.8
49–50	0.9	2.3	2.3	1.9	2.2	2.7	3.4	5.7	3.1	3.0	4.5	0.9	2.7
48–49	0.9	2.8	1.2	1.5	2.7	2.4	3.0	5.7	4.3	4.4	4.9	3.2	3.1
47–48	0.5	3.7	2.5	2.4	2.7	1.9	2.6	1.0	4.3	3.3	2.1	1.4	2.3
46–47	1.0	1.9	2.7	3.0	3.0	3.1	3.0	4.7	6.3	4.5	4.1	2.7	3.3
45–46	1.0	2.5	4.0	4.0	2.6	1.9	6.9	3.8	7.0	4.4	7.0	6.8	4.3
44–45	0.7	3.3	2.9	3.1	3.5	5.3	8.2	7.6	8.2	5.9	7.0	7.2	5.2
43–44	0.9	2.2	3.4	2.3	3.9	4.3	7.7	4.7	5.9	3.8	5.4	6.3	4.2
42–43	0.6	1.2	2.3	2.3	3.7	2.7	4.7	0.0	3.5	3.8	2.9	5.4	2.8
41–42	3.3	3.6	6.5	4.8	6.9	7.2	8.6	1.9	3.9	7.0	7.0	6.3	5.6
40–41	8.0	6.0	12.5	5.7	11.6	13.5	9.4	6.7	5.1	8.7	8.6	9.9	8.8
39–40	2.5	2.9	5.1	3.5	4.5	5.3	3.9	7.6	8.2	2.1	2.9	5.9	4.5
38–39	5.1	3.3	5.0	4.8	3.5	5.8	3.4	1.9	3.9	3.3	4.1	3.6	4.0
37–38[b]	22.5	10.4	5.6	8.7	5.7	3.4	4.7	13.3	5.1	5.4	5.8	5.9	8.0
36–37	23.9	12.2	12.3	10.3	8.4	6.7	6.4	7.6	3.5	8.5	5.4	7.2	9.4
35–36	13.2	10.2	10.0	9.5	6.3	7.9	3.4	2.8	0.8	9.9	7.0	5.9	7.3
34–35	7.0	9.3	7.1	10.0	7.8	5.8	3.0	5.7	2.5	8.5	2.1	4.1	6.1
33–34	1.2	2.2	1.5	3.0	1.4	2.4	1.3	1.0	1.2	1.4	2.1	0.4	1.6
32–33	0.5	0.6	0.5	1.4	0.6	0.5	0.0	2.9	0.4	0.7	1.6	0.0	0.8
31–32	0.2	0.5	0.3	0.9	0.0	0.2	0.4	1.0	3.5	1.0	1.2	0.0	0.8
30–31	1.0	1.3	0.5	0.6	0.2	0.2	0.4	0.0	3.1	1.2	1.2	3.2	1.1
29–30	0.4	1.5	1.0	0.5	1.0	1.2	0.9	1.0	1.6	1.4	1.2	3.2	1.2
Total	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*

[a] Figures in parentheses represent number of recoveries.

[b] Union County Refuge.

Table 14. Unlike results from previous banding stations in Illinois, smaller proportions of recoveries occurred in the latitude of the banding station. The average was only 8.0 percent for the entire period as contrasted with 19.6 percent for the return of Chautauqua mallards to the latitude of their banding station. Combining of mallard recoveries from the latitude of the Union County banding station with the latitude immediately to the south results in a 17.4 percent return. At other Illinois stations the combined recoveries of 2 degrees embracing the banding station varied from 22 to 25 percent.

The difference in return of mallards to the Union County area from that at other Illinois areas is, in our opinion, due to the differences in migration response when overflights occur. The Union County area is on the northern fringe of the main wintering grounds for the mallard in the Mississippi Flyway. We speculate that when mallards bound for the Union County area miss it, perhaps flying over on dark nights, they reach their main wintering grounds instead of their more immediate destination. Apparently because these ducks find themselves on a wintering area with which they are familiar, there is no sizeable reversal of direction. They are content to remain where they are. Banded mallards of Union County spend more time on their main wintering grounds than those banded elsewhere in Illinois. For example 22.8 percent of the indirect recoveries from Union County bandings, 1955–1966, occurred between 34° and 37° of latitude, the principal wintering area in the Mississippi migration corridor (Bellrose 1968). During the same years, only 15.7 percent of the Chautauqua recoveries occurred between the 34° and 37° parallels.

We know, from many field observations, that when mallards bypass Lake Chautauqua or some other migration stop, large numbers return to the bypassed area (Bellrose 1966:80), usually in the evening following their arrival. This reverse flight is occasionally observed on the wintering grounds in Arkansas, but it is most infrequent when compared to that observed in migration areas. Thus, we conclude that an overflight of mallards at Union County would not result in the same degree of return as when this event occurs at migration areas farther north in Illinois.

Delta Marsh Bandings

(During the fall seasons, 1947–1953, Arthur S. Hawkins of the U.S. Bureau of Sport Fisheries and Wildlife, and personnel of the Delta Waterfowl Research Station banded mallards at the Delta Marsh, Manitoba, Canada. The Delta Marsh embraces about 30,000 acres of shallow water and vegetation at the lower end of Lake Manitoba, some 60 miles west-northwest of Winnipeg, Manitoba. Most of the mallards frequenting the Delta Marsh in the fall have migrated to it from farther north. Delta Marsh is on the eastern fringe of the main breeding grounds of the mallard, and although some of the birds nest there, the bulk of the fall population is transient.)

Longitudinal Distribution. — The mean lines of the longitudinal distribution of recoveries from mallard bandings at the Delta Marsh are shown for both direct and indirect recoveries in Fig. 15.

The direct and indirect recoveries of mallards banded at the Delta Marsh show a similar longitudinal distribution; there are a few minor variations between the axial line formed by direct recoveries and the axial line formed by indirect recoveries. The close agreement between the longitudinal distribution of direct and indirect recoveries shows that after mallards have once made the flight down the flyway they conform in subsequent years to almost identical migration patterns.

The distribution of indirect band recoveries from Delta Marsh mallards,

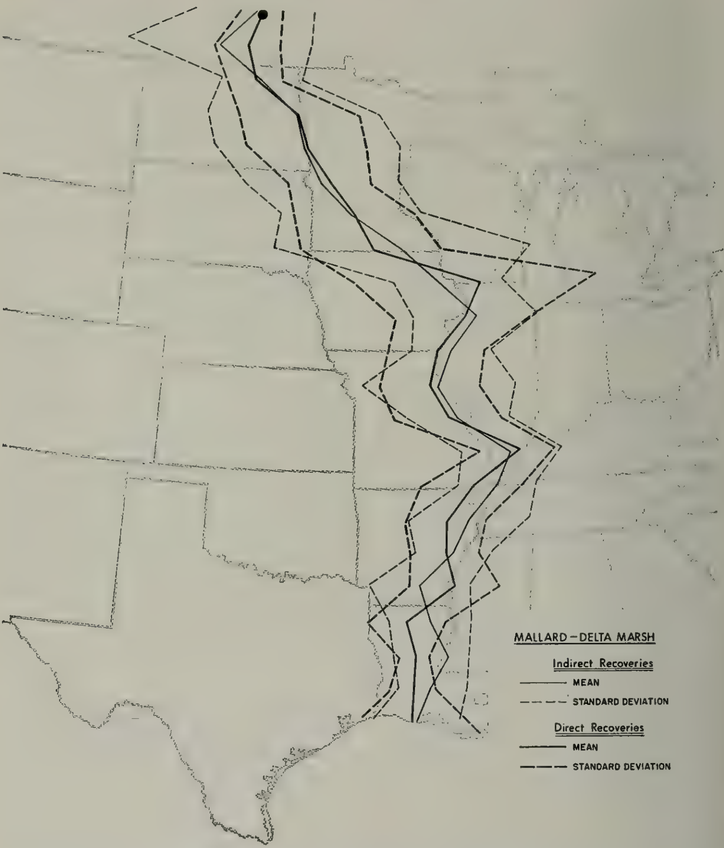

Fig. 15. — The longitudinal distribution of mallard indirect recoveries as compared with direct recoveries on the basis of mean and standard deviation lines. Mallards banded at the Delta Marsh, Manitoba, Canada, 1947–1953.

south of the Canadian border, is almost identical to that obtained from indirect recoveries of mallards banded in Illinois. The only important geographic difference between Illinois recoveries and those at Delta Marsh occurs in the region of the Delta Marsh. Recoveries from bandings of mallards in Illinois show that axial recovery lines occur west of the Delta Marsh on a northwest-southeast slant from central Saskatchewan to Illinois. Thus, mallards once having made Delta Marsh a migration stop evidently move eastward from the main stream of the southeastward passage to return to Delta. Upon departing Delta Marsh, these mallards rejoin the main stream of migrants in the Mississippi corridor by the time the border of the United States is reached.

A comparison of the longitudinal distribution of direct and indirect mallard recoveries in relation to their banding at the Delta Marsh is presented in Table 15. There are some variations in the mean longitude of indirect recoveries as compared with those for direct recoveries. In 3 of the years, the standard deviation showed a clustering of indirect recoveries around Delta almost as compact as for direct recoveries. However, in 1949 and 1952 there was a much wider dispersion in indirect recoveries.

Table 15. — A comparison of the longitudinal distribution of direct and indirect mallard recoveries, 1948–1953, from bandings at the Delta Marsh, Manitoba, Canada. Recoveries for the degree of latitude of the banding station (50°–51°). Banding station located at about 98.3° longitude.[a]

	Direct Recoveries		*Indirect Recoveries*	
Year	Mean	Standard Deviation	Mean	Standard Deviation
1948	98.54	0.50	...	...
1949	98.76	0.97	99.50	2.28
1950	98.57	0.63	97.81	0.98
1951	98.83	1.06	99.93	1.16
1952	98.89	1.36	98.86	4.30
1953	98.68	0.95	98.75	1.16
Average	*98.71*		*98.97*	

[a] 1 degree of longitude at this latitude equals about 45 statute miles.

Latitudinal Distribution. — The latitudinal distribution of both direct and indirect recoveries from mallards banded at Delta Marsh is shown in Table 16. About 40 percent of all direct recoveries occurred at the latitude of the banding station. This is substantially below the average of 55 percent for direct recoveries of Illinois bandings recovered in their home latitudes.

Table 16. — A comparison of the distribution of direct and indirect recoveries for the same latitudes from north of the banding station at Delta Marsh, Manitoba to the Gulf of Mexico, 1947–1953.

Degree of Latitude	*Direct Recoveries*		*Indirect Recoveries*	
	Number	Percent	Number	Percent
55–56	...	...	2	0.4
54–55	...	...	1	0.2
53–54	...	...	3	0.7
52–53	...	...	6	1.3
51–52	13	1.3	16	3.5
50–51[a]	411	39.9	87	19.2
49–50	41	4.0	20	4.4
48–49	35	3.4	20	4.4
47–48	16	1.6	12	2.6
46–47	21	2.0	9	2.0
45–46	48	4.7	24	5.3
44–45	43	4.2	21	4.6
43–44	23	2.2	19	4.2
42–43	14	1.4	13	2.9
41–42	39	3.8	17	3.8
40–41	25	2.4	13	2.9
39–40	41	4.0	19	4.2
38–39	17	1.7	7	1.5
37–38	16	1.5	12	2.6
36–37	33	3.2	26	5.7
35–36	53	5.1	21	4.6
34–35	39	3.8	37	8.2
33–34	22	2.1	9	2.0
32–33	16	1.5	7	1.5
31–32	7	0.7	4	0.9
30–31	22	2.1	6	1.3
29–30	35	3.4	23	5.1
Total	*1,030*	*100.0*	*454*	*100.0*

[a] Delta Marsh.

The distribution of direct recoveries by latitude indicates that when mallards left the Delta Marsh they migrated to many diverse places. No single latitude had a monopoly on recoveries; rather there was an astonishingly even dispersion by latitude down the flyway.

Indirect recoveries in the latitude of the Delta banding station (50°–51°) compose about one-fifth of recoveries for all latitudes. This is almost identical to that found for indirect band recoveries of mallards in the latitude of their respective banding stations in four regions of northern and central Illinois. It is double that found for mallards returning to the vicinity of their banding station at the Union County Refuge in southern Illinois.

A comparison of the proportions of direct and indirect recoveries (Table 16) at the latitude of the Delta Marsh banding station discloses that at this latitude direct recoveries are twice as important as indirect recoveries. Here again, as at Illinois banding stations, it is evident that only about half of the mallards visit the same latitude for comparable periods of time as in the year in which they were initially banded. This suggests that overflights occur among a sizeable proportion of previous autumn inhabitants. As noted earlier, there is some return from overflights, but apparently it is not sufficient to greatly compensate for all that pass by.

The percentage of indirect recoveries on the wintering grounds for the Delta banded mallards (29°–37°), is 1.3 times greater than for the direct recoveries. This implies that mallards which pass over the Delta Marsh spend most of the additional time gained by such passage (23 percent) on the wintering grounds rather than on migration areas between the Delta Marsh and wintering grounds in Arkansas.

Squaw Creek Wildlife Refuge Bandings

(The Squaw Creek National Wildlife Refuge covers 6,800 acres of land and water a few miles east of the Missouri River near Mound City in northwestern Missouri. At the time of the bandings, 1937–1963, Squaw Creek was the only significant concentration point for mallards along the Missouri River between Sioux City, Iowa, and Kansas City, Missouri. Because of the paucity of waterfowl habitat in this region, tremendous concentrations of mallards developed during the fall migration. In most Novembers, mallards numbered between 200,000 and 400,000, and, along with other ducks, and tens of thousands of lesser snow geese, created a tremendous congestion of waterfowl. The De Soto National Wildlife Refuge, established in 1958, is located on the Missouri River, 20 miles north of Omaha, Nebraska. Appreciable numbers of mallards did not begin to frequent this refuge until 1963.)

Longitudinal Distribution. — The longitudinal distribution of mallard indirect recoveries between central Saskatchewan and southern Louisiana is shown for Squaw Creek bandings in Fig. 16. The axial and standard deviation lines are similar in southern Canada to those for Illinois banding stations. Thus, up to this point, mallards from all the various banding stations discussed appear to originate from the same region of the central Saskatchewan plains.

South of the Canadian border, the path of band recoveries, as delineated by the longitudinal distribution of about two-thirds of them, extends on a bearing of about 155 degrees to east-central Arkansas. There the course changes to south, terminating on the Gulf Coast marshes in western Louisiana.

The zigzags in this mapped path of band recoveries (Fig. 16) are largely the result of differences in the longitudinal distribution of waterfowl habitat. The extensive waterfowl habitat along the Mississippi River from southern Minnesota to St. Louis exerts an influence on the longitudinal mean and standard deviation. Because of the influence of the Mississippi River, the axial line is pulled eastward from what is undoubtedly the true path used by this population element of mallards. For example, at the latitude of the Squaw Creek banding station, the *mean* longitude of indirect recoveries is 50 miles to the east, yet the longitudinal *median* of the indirect recoveries occurs within a few miles of the banding station.

The southern Arkansas and northern Louisiana wintering grounds area for Squaw Creek mallards is a short distance to the west of the region occupied by mallards banded at Illinois stations (Fig. 25).

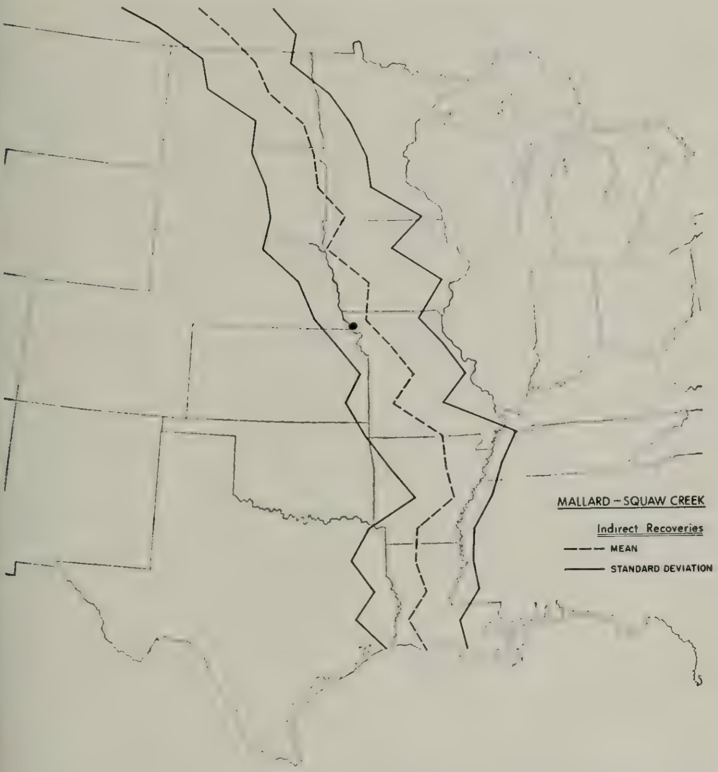

Fig. 16.—The longitudinal distribution of mallard indirect recoveries on the basis of mean and standard deviation lines. Mallards banded at the Squaw Creek National Wildlife Refuge, Holt County, Missouri, 1937–1963.

Latitudinal Distribution.—Indirect recoveries of mallards banded at Squaw Creek are rather evenly distributed down the flyway (Table 17) except at the latitude of the banding station and on the principal wintering grounds. For mallards returning to the vicinity of the banding station the indirect recovery rate at the station latitude was more than twice that for any latitude to the north. Because the banding station was located only a few miles north of the 40° parallel, we included recoveries from the adjacent degree of latitude to the south. The combined total for the 2 degrees of latitude was 16.3 percent compared to 22 to 25 percent for comparable areas at Delta Marsh, Manitoba, and the four stations in northern and central Illinois.

We believe that the lower proportion of indirect band recoveries, within the home range of Squaw Creek mallards, results from the tremendous concentra-

Table 17.—The number and percent of indirect recoveries, 1938–1966, by degrees of latitude from mallards banded at the Squaw Creek National Wildlife Refuge, Holt County, Missouri (40°–41°). Station located at about 95.3° longitude.

Degree of Latitude	*Recoveries*	
	Number	Percent
55–56	2	0.1
54–55	23	1.2
53–54	55	2.9
52–53	78	4.1
51–52	72	3.8
50–51	76	4.0
49–50	83	4.4
48–49	62	3.3
47–48	56	3.0
46–47	50	2.7
45–46	56	3.0
44–45	66	3.5
43–44	53	2.8
42–43	50	2.7
41–42	97	5.1
40–41[a]	217	11.5
39–40	91	4.8
38–39	66	3.5
37–38	39	2.1
36–37	83	4.4
35–36	126	6.7
34–35	204	10.8
33–34	42	2.2
32–33	32	1.7
31–32	21	1.1
30–31	48	2.5
29–30	39	2.1
Total	*1,887*	*100.0*

[a] Squaw Creek Refuge.

tion there. At times, the population density of mallards is so great (200 per acre of water) that the carrying capacity of the refuge is sorely overtaxed. This tremendous density probably induces many ducks to move on down the flyway sooner than if densities were less. The differences in the latitudinal distribution of indirect recoveries between Chautauqua and Squaw Creek banding stations lend credence to this contention.

Both banding stations are between the 40° and 41° parallels. All of the indirect recoveries north of this latitude amounted to 46.6 percent for Squaw Creek (Table 17) and 45.6 percent for Chautauqua (Table 2), almost identical. Yet, south of the banding station the recoveries amounted to 41.9 percent for Squaw Creek mallards (Table 17) but only 34.0 percent for Chautauqua mallards (Table 2). The differences in band recovery rates south of the respective banding stations imply differences in the relative time the mallards of each banded group spent on their principal wintering grounds. Squaw Creek mallards spent 19 percent more time on the wintering grounds than did those banded at Lake Chautauqua. It appears that Squaw Creek mallards departed after a shorter stay than customary at migration stopovers at Delta, Manitoba, and northern and central Illinois.

Black Hills Bandings

(Personnel of South Dakota's Department of Game, Fish, and Parks banded 2,144 mallards in the northern Black Hills during the winters of 1950–1951 and 1951–1952 (Drewien 1968). One banding station was located on Coxy's Lake, 7 miles northwest of Spearfish, South Dakota, the other station was on Bear Butte Lake, 7 miles northeast of Sturgis. Warm springs have enabled from 6,000 to more than 30,000 mallards (average 16,500) to winter at this northern outpost, 1963–1968.)

The latitudinal distribution of indirect recoveries from mallards banded in the Black Hills (Table 18) has been adapted from data reported by Drewien (1968). Quite different from other banding stations was the fact that 46.4 percent of the indirect recoveries from bandings in the Black Hills occurred at the same latitude as the banding station and only 22.0 percent occurred south of the banding station. The recovery rate south of the Black Hills banding station was considerably lower than the 41.9 percent south of the Squaw Creek station and the 34.0 percent south of the Lake Chautauqua station. Moreover, at the latitude of the banding station the longitudinal distribution of recoveries was confined, with only a few exceptions, to

Table 18. — The number and percent of indirect mallard recoveries by degrees of latitude from bandings during the winters of 1950–1951 and 1951–1952 in the northern Black Hills, Lawrence County, South Dakota.[a] Stations located at about 103.8° longitude.

Degree of Latitude	*Recoveries*	
	Number	Percent
55–56	1	0.3
54–55	5	1.6
53–54	9	2.8
52–53	13	4.1
51–52	9	2.8
50–51	20	6.3
49–50	16	5.0
48–49	11	3.4
47–48	3	0.9
46–47	10	3.1
45–46	4	1.3
44–45[b]	148	46.4
43–44	6	1.9
42–43	6	1.9
41–42	19	5.9
40–41	5	1.6
39–40	5	1.6
38–39	1	0.3
37–38	2	0.6
36–37	4	1.3
35–36	7	2.2
34–35	8	2.5
33–34	1	0.3
32–33	1	0.3
31–32	1	0.3
30–31	0	0.0
20–30	4	1.3
Total	*319*	*100.0*

[a] From "Recovery Analysis of Mallards Banded in the Black Hills During the Winters of 1950–51 and 1951–52," by Rod C. Drewien. Pittman-Robertson Project W-75-R-10. Report of South Dakota Department of Game, Fish and Parks.

[b] Black Hills banding station.

within the degree of longitude (103°–104°) containing the banding areas. Such distribution in the indirect recoveries points to the strong homing of mallards back to this particular wintering area. This wintering area is far north of the principal wintering grounds of the mallard. It is comparatively small, and isolated from other waterfowl habitat.

The isolated nature and northern location of this wintering area are believed responsible for the unusually large proportion of indirect recoveries in the vicinity of the banding station. Because of the limited waterfowl habitat in the Black Hills region of South Dakota, it is more essential for mallards to return to a specific locality than in regions where habitat is more widespread. Because of the northern location, latitudinal distribution is restricted to a greater degree than at other banding stations in this study. These mallards migrated over a much shorter distance to reach their winter quarters than customary for the species in the Mississippi migration corridor.

Obviously not all the mallards that wintered in the northern Black Hills during the years of banding (1950–1951 and 1951–1952) elected to winter there in subsequent years. Slightly less than one-third moved south of the Black Hills during subsequent hunting seasons. However, the single greatest concentration of recoveries occurred only a short distance south of the Black Hills along the North Platte River of western Nebraska.

Seasonal Turnover in Population

It is important to ascertain the seasonal turnover in migratory waterfowl populations as an aid in evaluating population status and determining food and space requirements of migrating populations. We analyzed direct band recoveries and repeats of banded mallards with this objective in view. Then we also analyzed the latitudinal distribution of indirect recoveries as a means of determining the time spent by mallards at a migratory area.

Direct Recoveries. — Fig. 17 shows the relationship of time following banding to direct recoveries by age and sex classes of mallards at latitudes from the Lake Chautauqua banding station south. The mean recovery of bands at the latitude of the banding station occurred from 14.9 days after banding for juvenile drakes to 17.3 days for adult drakes and 16.0 days for hens of all ages. The progression of band recoveries southward was almost linear between time

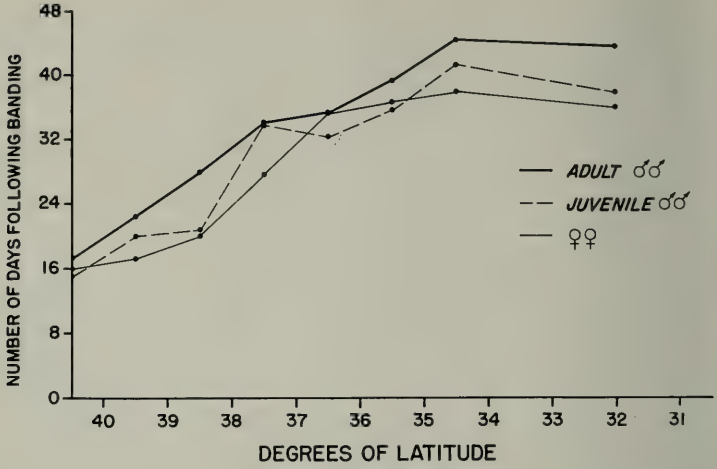

Fig. 17. — The mean southward passage of adult drake, juvenile drake, and hen mallards in relation to time as determined from direct band recoveries of ducks banded during the fall, 1939–1944, 1947–1952, at Lake Chautauqua.

and distance until the latitude of 34.5°. From that region (Stuttgart, Arkansas) southward, there was a plateau in time versus distance for all three classes of mallard band recoveries. We deduce that mallards migrating to the southern region of the wintering grounds did so by passing over the central region of the wintering grounds from a migration area between Lake Chautauqua and the wintering area.

The passage of mallards between the area of the banding station and the principal wintering grounds (Stuttgart, Arkansas, region of the Mississippi migration corridor) took varying amounts of time for the different age and sex classes. The elapsed time for adult drake band recoveries (Fig. 17) between the banding station mean and wintering grounds mean was 27 days. For juvenile drakes the elapsed time was 26 days, and for hens of all ages 22 days.

However, the percentage grouping of band recoveries based on the intensity of recovery by time versus distance (Fig. 18), shows that there is a great variation in the individual rate of passage southward — some mallards moved into northern Louisiana (33°–32°) within 6 days after bandings; other mallards were still in the vicinity of the banding station over 60 days after banding.

Fig. 18 gives the impression that rather than a methodical passage southward mallards migrate by considerable leapfrogging. That is, when a migratory movement occurs, certain elements of the mallard population fly to waterfowl habitat in the latitude immediately to the south, others continue to habitats 2 degrees southward, others continue to habitats 3 degrees southward, and so on until the southern limits of the wintering grounds are reached. Nevertheless, there is a tendency for the largest proportion of migrating mallards to drop out of southward flight at the shorter ranges while smaller proportions continue to the more extreme ranges. Thus, in Fig. 18, even with the evidence of a great spread in individual migratory

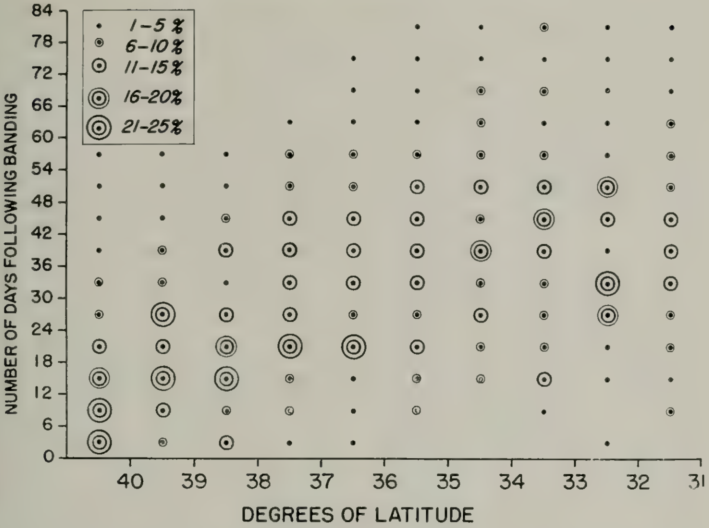

Fig. 18. — The percentage grouping of mallard recoveries, based on time versus distance, showing the variation in individual rate of passage southward. Mallards banded at Lake Chautauqua, 1939–1944, 1947–1952.

behavior, there is an evident relationship in recoveries between time and distance.

It also seems apparent that there is a seasonal relationship between time and distance traveled. Table 19 shows the mean miles per day traveled by age and sex classes of seasonally banded samples of mallards. Miles per day were derived from the distance of the banding station to location of the band recovery in relation to time.

The low rate of movement during the

Table 19. — Seasonal change in rate of passage of mallard age and sex groups from Lake Chautauqua, 1939–1944. Based on distance traveled in relation to number of days from banding for direct recoveries, and expressed in mean number of miles per day.

Week of Banding	*Adult Drakes*		*Juvenile Drakes*		*Hens*	
	Number	Miles per Day	Number	Miles per Day	Number	Miles per Day
Oct. 11–17	28	4.2	58	3.4	44	5.2
" 18–24	58	5.2	62	4.2	57	5.7
" 25–31	73	5.8	82	6.9	35	6.0
Nov. 1– 7	69	6.0	89	5.5	48	7.4
" 8–14	109	6.3	30	7.2	43	8.5
" 15–21	87	10.1	76	7.6	24	10.0
" 22–28	88	9.4	75	9.7	51	11.3
" 29–Dec. 5	34	12.0	30	14.5	26	14.2
Average		*7.4*		*7.4*		*8.5*

first 2 weeks (October 11–24) might have been partly determined by the opening of the Illinois hunting season, which occurred on either October 15 or 16 except in 1939 when it did not open until October 22. During this time period some of the banded mallards were not immediately exposed to hunting, and undoubtedly this slightly lowered the rate of daily movement. In a similar way, the rate of passage late in November was probably biased toward a higher rate by the Illinois closure of the hunting season, which occurred between December 5, 1939 and January 1, 1944. Hence, more distant mallards were likely to be shot than were mallards near the banding station.

The rate of movement of mallards as expressed for the weeks from October 25 through November 21 appears little affected by the opening or closing of the hunting season. Examining data for this period only, we find that adult drake mallards averaged 7.5 miles per day, juvenile drake mallards averaged 6.8 miles per day, and hens averaged 8.0 miles per day. Within this period, the rate of movement increased as the season progressed: adult drakes from 5.8 to 10.1 miles per day, juvenile drakes from 5.5 to 7.6 miles per day, and hens from 6.0 to 10.0 miles per day.

The departure of mallards from the immediate area of the banding station has been evaluated by two types of data: 1) a time-related shrinkage in band recoveries within the degree of latitude embracing the banding station, and 2) the interval of time between the initial banding and the last recapture of a mallard at the same banding station during the same season.

Fig. 19 shows the length of time mallards remained in the vicinity of the banding station at Lake Chautauqua, based on band recoveries of both shot and retrapped mallards. The lines of shrinkage in numbers of banded ducks within the trapping zone are curvilinear for both shot and retrapped recoveries. Because there is a curvilinear rather than a linear relationship to time, the medians show shorter time spans in the area of the banding station than do the means in Fig. 17. The median number of days, as determined for shot recoveries within the latitude of trapping, was 12.0 for adult drakes, 10.0 for

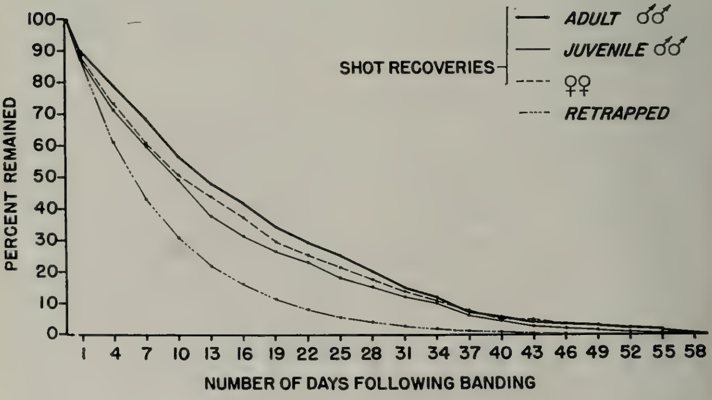

Fig. 19.—The length of time mallards remained in the vicinity of the banding station at Lake Chautauqua, based on shot recoveries from hunters and repeats of live ducks at banding traps.

hens, and 9.5 for juvenile drakes. The median number of days for the last retrapping of individual mallards of all ages and both sexes was only 6 days.

The skewing of the band recovery curves, as related to the passing of time, points to this axiom: the longer a mallard remains in the area of Lake Chautauqua, the greater the likelihood of it remaining longer. Both shot recoveries and retrap data indicate that the likelihood of departure was greatest soon after banding and decreased progressively with the passing of time.

Further analysis of banded mallards retrapped (the repeats) provides additional appraisals on the duration of time spent in the vicinity of the banding station. Tables 20 and 21 present data on the seasonal change in the mean days between banding and the last day the same individuals were recaptured. A time span of 3 weeks was provided beyond the banding dates shown in Tables 24 and 25 for ducks to be recaptured. There is evidence that early in the migration season mallards tend to remain slightly longer in the banding area than they do late in the season. This is in agreement with shot band recovery data (Table 19) which showed fewer miles per day of movement early in the migration season.

Mallard repeats at both Lake Chautauqua and Spring Lake remain in the vicinity of the banding station about 10–12 days (Tables 20 and 21). This is somewhat less than the mean span derived from shot recoveries, which was 17.3 days for adult drakes, 14.9 days for juvenile drakes, and 16.0 days for hens.

After a banded duck is released, two

Table 20. — Seasonal changes in the mean number of days mallards were last retrapped following their initial banding at Lake Chautauqua in the years 1940–1943.

Week of Banding	*1940*		*1941*		*1942*		*1943*		*Average Mean Days*
	Number Retrapped	Mean Days	Number Retrapped	Mean Days	Number Retrapped	Mean Days	Number Retrapped	Mean Days	
Oct. 4–10	...	...	...	...	39	13.4	...	...	13.4
" 11–27	193	9.0	...	...	82	11.3	37	12.5	10.9
" 18–24	55	9.6	...	...	264	8.3	271	13.0	10.3
" 25–31	50	14.2	...	...	162	7.7	164	10.1	10.7
Nov. 1– 7	64	13.5	39	11.8	168	7.8	138	10.6	10.9
" 8–14	40	13.9	73	11.1	...	...	270	9.0	10.3
" 15–21	58	5.4	43	9.0	...	...	...	...	7.2
Average		*10.9*		*10.6*		*9.7*		*11.0*	*10.5*

Table 21. — Seasonal changes in the mean number of days mallards were last retrapped following their initial banding at Spring Lake Refuge, Carroll County, Illinois in 1946 and 1947.

Week of Banding	*1946*		*1947*		*Average Mean Days*
	Number Retrapped	Mean Days	Number Retrapped	Mean Days	
Oct. 11–17	45	13.6	...	...	13.6
" 18–24	112	14.3	...	...	14.3
" 25–31	147	12.0	113	9.4	10.7
Nov. 1– 7	251	8.2	112	9.2	8.7
Average		*12.0*		*9.3*	*11.8*

counteracting forces affect its potential recapture; they are 1) desire to return for bait, and 2) fear of being recaptured. Apparently the fear of the trap is greater than the desire for bait because the interval of repeats is 6 days less than the interval of recoveries from shot ducks.

We can only speculate on the length of time a mallard was present in the area prior to its capture and banding. A clue lies in the difference in the span of time between recoveries of mallards shot in the vicinity of the banding station and those recaptured in the banding traps. If we assume that the banding traps are equally effective at capturing both newly arrived and previously banded mallards, then the difference in departure intervals between shot and retrapped recoveries can be employed. Band recoveries from shot mallards in the latitude of the banding station show a 6-day longer time span than do recoveries from retrapped birds. If we assume this ineffectiveness in capturing newly arrived birds, the potential sample of mallards is present on Lake Chautauqua an average of 6 days prior to initial banding. Thus with the 16 days the banded birds are present following banding there is an average span of 22 days between arrival of the birds and their departure from the area.

Analysis of indirect recoveries for population turnover, discussed below, indicates that the 6 days for the pretrap period is too low. It is probably closer to 12 days.

Indirect Recoveries.—Information on the length of time mallards remain at any single location during migration can also be derived from the relative proportion of indirect recoveries in any 1 degree of latitude. The latitudinal distribution of band recoveries reflects the time mallards spend at any specific latitude. Shooting pressure on mallards appears quite uniform geographically between southern Saskatchewan and Louisiana. This has been demonstrated by the remarkably similar band recovery rates of mallards near every banding station discussed in this paper. Therefore, within the scope of this study, the geographic distribution of recoveries broadly represents the length of time mallards spend during the hunting season in any defined geographic area.

Hunting seasons on mallards in the Mississippi Flyway of the United States during the years 1940–1960 have ranged from 92 to 107 days. The season in Canada has usually opened 10–15 days earlier than in the United States, almost always on September 15. Seasons in the United States have generally opened October 1–October 8 and closed January 8–January 15, depending upon the length of the season. Band recoveries from mallards shot in September amount to less than 5 percent of the total indirect recoveries from Illinois banding. Over the years about 95 percent of the mallard indirect recoveries have occurred over a 100-day period, October 1–January 8. Thus 1 percent in latitudinal distribution of band recoveries represents 0.95 day during the hunting season.

Equating the proportion of mallard indirect recoveries, within the latitudes of their respective banding stations, to the duration of stay in the hunting season provides data for several deductions. Lake Chautauqua mallards, 1940–1966, (Table 2) spent an average of 18.6 days (0.95 x 19.6) within the degree of latitude where banded in previous years. McGinnis Slough banded mallards (Table 7) spent an average of 15.9 days in the area of their station in years following banding. Spring Lake mallards (Table 10) spent 22.2 days within 1 degree of latitude above and below where banded in previous years. Calhoun Refuge mallards (Table 12) spent 22.7 days in subsequent years within 1 degree of latitude above and below their banding station. Union County banded mallards (Table 14) spent 16.5 days within 1 degree above and below the banding station in years following banding. Delta Marsh, Manitoba, banded mallards (Table 16) spent an average of 18.2 days in subsequent years within the same degree of latitude as their banding station.

As discussed earlier, direct band recoveries indicated that Lake Chautauqua mallards remained 22 days in the vicinity of the banding station. Indirect recovery data from the same station indicated that mallards remained 18.6 days.

However, it must be kept in mind that indirect recoveries from Lake Chautauqua were 1.5 times more numerous on the wintering grounds than were direct recoveries. This was interpreted as the result of overflights by certain groups of mallards which proceeded directly to the wintering grounds without stopping more than momentarily at one of their traditional marshes. If this is indeed the behavior that occurred, then those mallards that did halt their southward flight at their traditional marshes (as shown by direct recoveries) remained a longer period than the calculated 18.6 days (as determined from indirect recoveries). The 18.6 days represent the functional stay of the entire population at a traditional migration area, as measured by indirect recovery data. Since a certain proportion of the migrants bypassed the migration area, those that did stop (direct recovery data) more than momentarily at their traditional areas remained 1.5 times the number of days indicated by the performance of the entire population (indirect recovery data). Therefore, those mallards that did return to their traditional areas remained 1.5 x 18.6 days or 27.9 days.

We conclude that mallards in the Mississippi migration corridor remain about 28 days at each traditional migration area they use between their breeding and wintering grounds. The relative time mallards from the several banding stations in the Mississippi migration corridor remain on breeding grounds, migration areas, and wintering grounds between October 1 and January 8 is shown in Table 22. The delineation of these regions by latitude is somewhat arbitrary for there is an overlap between breeding and migration areas as well as between migration and wintering areas. However, the bulk of the mallards in the Mississippi migration corridor breed north of the 49° parallel and winter south of the 37° parallel.

Table 22. — Number of days mallards remained in three regions of the Mississippi migration corridor during the 100-day period, October 1–January 8, as determined from indirect recoveries in all years resulting from bandings at the various stations listed.[a]

Banding Station	*North of 49° (Breeding Grounds)*	*49°–37° (Migration Areas)*	*South of 37° (Wintering Grounds)*
Lake Chautauqua	13.4	64.5	22.1
McGinnis Slough	9.6	68.0	22.4
Spring Lake	9.5	65.6	24.9
Calhoun Refuge	10.5	61.2	28.3
Union County	15.6	56.1	28.3
Delta Marsh	29.7	41.0	29.3

[a] Based on latitudinal distribution of indirect band recoveries derived from Tables 2, 7, 10, 12, 14, and 16.

Each banded contingent displayed differences in the time spent in the three regions, but the time spent on the wintering grounds during this October 1–January 8 period was most uniform for all banding stations. During the 100-day period, mallards spent more time on migration areas than on breeding or wintering areas. Time on the breeding grounds varied from 9.5 to 29.7 days for the several groups, and was much the longest for Delta Marsh, Manitoba, mallards because they were transients, utilizing a marsh on the breeding grounds as a traditional migration stop.

If we accept 28 days as the period Lake Chautauqua banded mallards remained in the banding vicinity, then the 64.5 days spent on migration areas (Table 22) suggest that these birds had two or three important feeding and resting areas between their breeding and wintering grounds. This would also apply to almost all of the other banded groups except for those at Delta Marsh. Because of the longer time the Delta

Marsh mallards remained in the breeding grounds region, they had time for only one or two major migration stops between the Delta Marsh and their wintering grounds.

Seasonal Chronology

The seasonal chronology in the number of indirect band recoveries illustrates the general chronology of waterfowl migration. A comparison in Illinois of the seasonal distribution of indirect band recoveries with population estimates of mallards pointed up three differences: 1) seasonal peaks in mallard populations were higher than those shown by band recoveries, probably because bag limits asserted a greater restriction on the kill when mallards were most abundant, 2) populations of mallards were also comparatively larger after the freeze-up, usually about December 1, than indicated by band recoveries because when mallards were restricted by ice to open holes on a few large lakes the opportunity for hunting was greatly reduced, 3) some mallard migration, although usually minor, occurred prior to the opening of the hunting season. Most states in the Mississippi Flyway adjust their hunting seasons to encompass the mallard flight to the extent they can do so within the length and framework of the season set by federal regulations.

In spite of the several ways in which the seasonal distribution in band recoveries failed to conform to mallard populations in Illinois, there was sufficient agreement to indicate that broad interpretations of seasonal movements could be deduced from band recoveries. Fig. 20 illustrates the seasonal distribution of band recoveries from four geographic zones of North America.

The northern zone included North and South Dakota, Minnesota, and Wisconsin. The central zone included Iowa, Illinois, Indiana, and Missouri. The southern zone embraced all states in the Mississippi migration corridor south of the central zone. The years 1940–1946 were selected from the 1940–1952 period because of the large number of recoveries and relatively long hunting seasons in those years.

The seasonal progression of mallards southward in the Mississippi migration corridor is most apparent even though

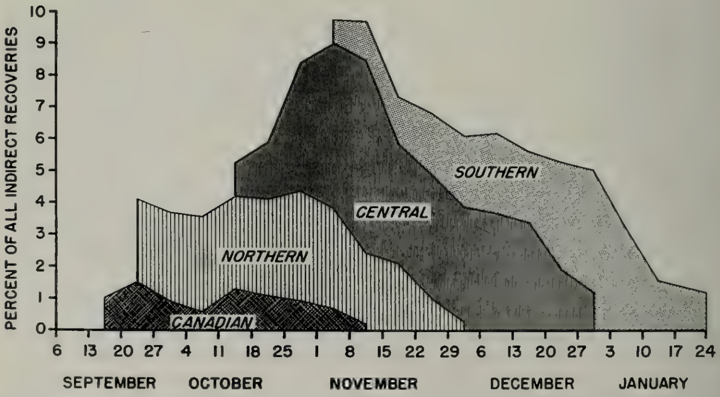

Fig. 20. — The seasonal distribution of indirect mallard band recoveries in four geographic zones of North America. Based on bandings at Lake Chautauqua, 1939–1944, and indirect recoveries, 1940–1946.

limited movements occurred during nonhunting periods. The passage of mallards into the northern zone is somewhat obscured by breeding birds already present in that zone together with an early passage into it from the Canadian zone prior to the hunting season.

Band recoveries suggest that mallard populations reached their greatest abundance in the various zones as follows: Canadian, September 20–26; northern, October 25–31; central, November 8–15; southern, December 27–January 3. The greatest time lag between periods of greatest abundance was between the central and southern zones, indicating

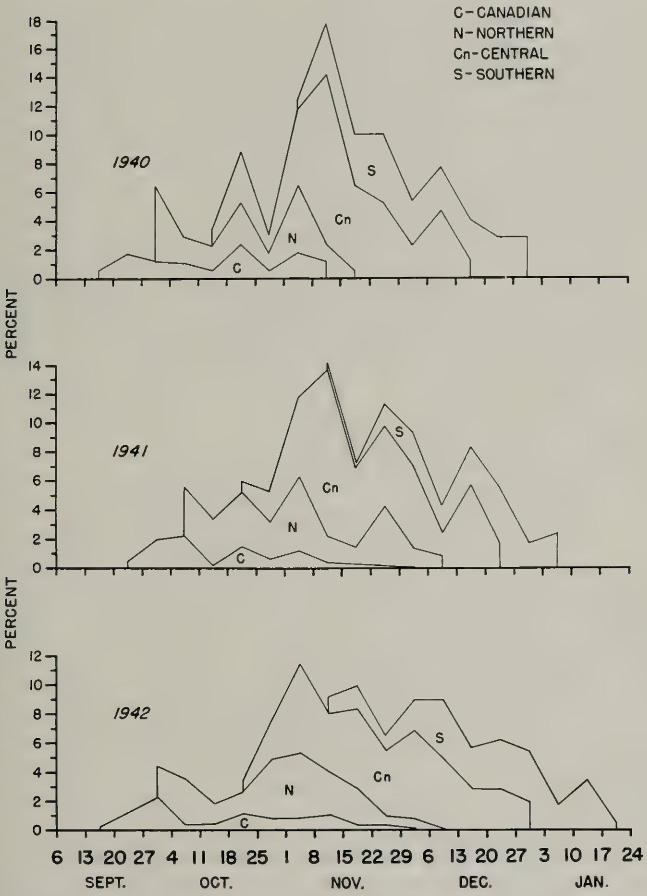

Fig. 21.—Yearly variation, 1940–1942, in the seasonal distribution of indirect mallard recoveries in four regions of North America.

that there was an early wave of migrants into the central zone which delayed departure to the southern zone.

The median period of band recoveries for the several zones was as follows: Canadian, October 11–17; northern,

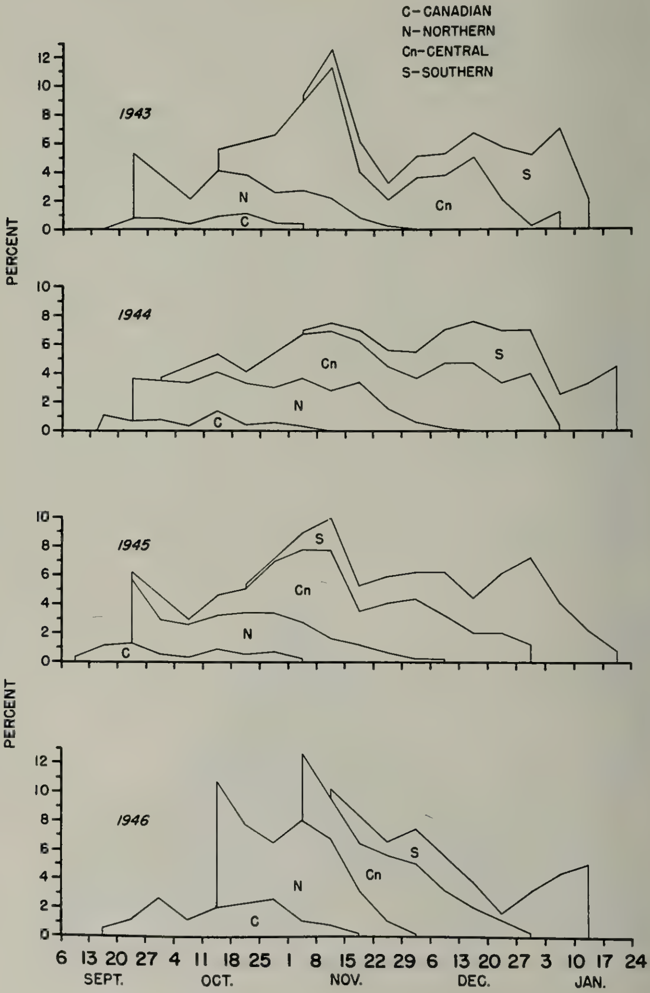

Fig. 22.—Yearly variation, 1943–1946, in the seasonal distribution of indirect mallard recoveries in four zones of North America.

October 18–24; central, November 15–21; and southern, December 13–19. Available evidence indicates that a 3½-month span occurred between the earliest passage from the Canadian zone to the last passage into the southern zone. The bulk of the southward passage occurred over a 2-month period, October 15–December 15.

In the period studied, 1940–1946, there is much variation among years in the chronology of recoveries from mallards (Fig. 21 and 22). Much of the variation in band recoveries reflects changes in the chronology of migration. Apparently the southward passage of mallards is greatly influenced by weather conditions, otherwise it would not be so variable from year to year.

Waves of migrants were most apparent in the central zone. Usually four waves were evident in that zone, three in the southern zone, and two to four in the northern zone. The primary waves of mallard migrants in the northern zone tended to center around the last week in September, with secondary waves usually centering around the second and the third weeks in October.

Largest waves of mallards tended to arrive in the central zone the first 2 weeks in November. The next largest waves, in order, tended to appear during the last 2 weeks in November and the first 2 weeks in December. Waves of migrating mallards varied so much in magnitude and time in the southern zone that it was not possible to classify their chronology. The largest waves of migrants arrived between December 2 and January 13. Waves of secondary magnitude occurred as early as November 4 and as late as December 30, and tertiary waves occurred between November 11 and January 6.

BLACK DUCK

(Illinois is on the western fringe of the black duck's range. Waterfowl censuses show a pronounced change in the abundance of black ducks between waterfowl habitats in the eastern and western regions of the state. For example, at McGinnis Slough in the Forest Preserve District of Cook County, 30 miles southwest of Chicago, black ducks were outnumbered by mallards by a ratio of 5:1. However, at Lake Chautauqua in central Illinois mallards usually outnumbered black ducks by a ratio of 50:1. Band recoveries indicate that most of the black ducks which migrate into Illinois originate from breeding grounds in the Laurentian Shield region of western Ontario. Human populations are sparse there, and as a result band recoveries are few in number and scattered. Hence, band recovery data from this region of Canada were too few to analyze for mean and standard deviation of recoveries by longitude and latitude.)

Lake Chautauqua Bandings

Between 1939 and 1952, 3,408 black ducks were banded at the Lake Chautauqua National Wildlife Refuge, Mason County, Illinois. The black ducks were trapped along with mallards in large, baited traps as previously described. Indirect recoveries have been analyzed within the United States by longitude and latitude with a view of determining the degree of homing back to the region of the banding station.

Longitudinal Distribution.—Recoveries from black ducks in the years following their banding at Lake Chautauqua have been analyzed for longitudinal mean and its standard deviation by degrees of latitude south of Canada (Fig. 23).

The axial and standard deviation lines, which denote the longitudinal distribution of the majority of the indirect band recoveries, indicate that most Lake Chautauqua black ducks moved into northwestern Minnesota from western Ontario and eastern Manitoba (Fig. 23). They passed east-southeast to the upper peninsula of Michigan and northern Wisconsin. The bulk of this population

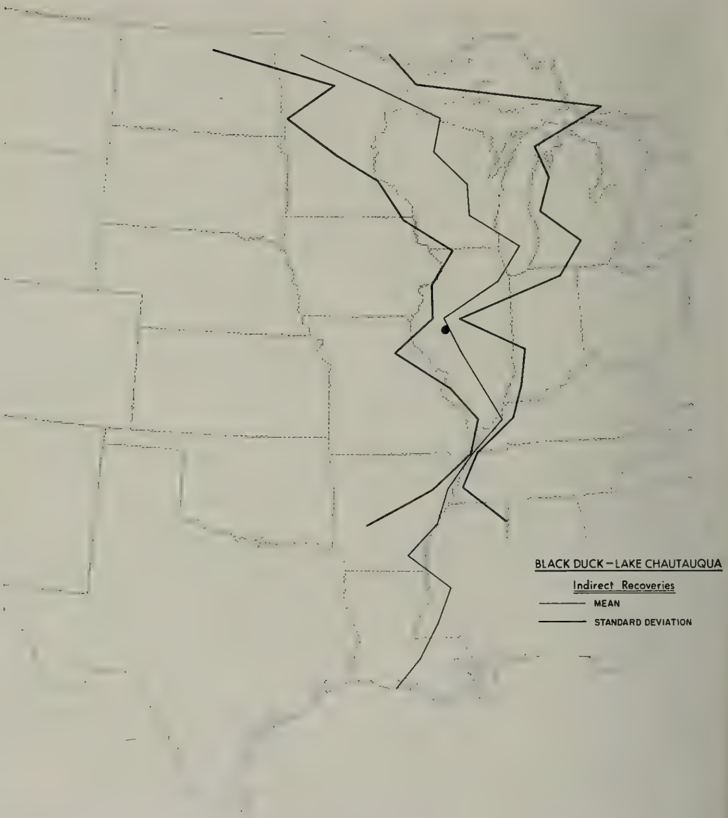

Fig. 23.—The longitudinal distribution of black duck indirect recoveries on the basis of mean and standard deviation lines. Black ducks banded at Lake Chautauqua, 1939–1944, 1947–1952.

of black ducks migrated south-southeast from north-central Wisconsin to northeastern Illinois. From that point, the center of the distribution approximated the course of the Illinois River valley to Lake Chautauqua.

Apparently on departing Lake Chautauqua most black ducks headed south-southeast for the area embracing the mouth of the Wabash River. South of this point, the axial line of recoveries was similar to the course of the Mississippi River. From Lake Chautauqua south, the distribution of black duck recoveries (Fig. 23) was very similar to that of mallards banded at the same place (Fig. 7). North of Lake Chautauqua, the indirect recoveries from black ducks were 200 or more miles east of those derived from mallards, reflecting the more eastward breeding range of the black duck.

The standard deviation lines denote a wide distribution of band recoveries in northern United States. It is assumed that this broad distribution of recoveries indicates that the Lake Chautauqua black ducks originated over an extensive breeding range. As the black ducks migrated south, toward Lake Chautauqua, the standard deviation lines converged in the area of the banding station to a breadth of only 44 miles. The spread in standard deviation for mallards at the same place was about 58 miles (Table 1).

South of southern Illinois to about Memphis, Tennessee, the standard deviation lines show very little spread in band recoveries. Beyond this point recoveries were widespread, and south of northern Mississippi they were so few in number as to be insignificant.

Latitudinal Distribution. — The latitudinal distribution of recoveries between the Canadian border and the Gulf of Mexico from black ducks banded at Lake Chautauqua is shown in Table 23.

Table 23. — The latitudinal distribution of indirect black duck recoveries, 1940–1952, from autumn bandings at Lake Chautauqua, Mason County, Illinois.

Degree of Latitude	*Number of Recoveries*	*Percent of Recoveries*
48–49	6	1.7
47–48	6	1.7
46–47	9	2.6
45–46	23	6.5
44–45	28	7.9
43–44	24	6.8
42–43	7	2.0
41–42	35	9.9
40–41[a]	128	36.3
39–40	16	4.5
38–39	4	1.1
37–38	19	5.4
36–37	12	3.4
35–36	9	2.6
34–35	17	4.8
33–34	1	0.3
32–33	1	0.3
31–32	3	0.8
30–31	4	1.1
29–30	1	0.3
Total	*353*	*100.0*

[a] Lake Chautauqua.

With 36.3 percent of the indirect recoveries at the latitude of the banding station, a very strong homing is indicated. It is also indicated that these black ducks spent about one-third of the hunting season within the United States in the vicinity of the Chautauqua refuge.

Apparently this population element of black ducks wintered farther north than did the population element of mallards banded at the same place. All indirect recoveries south of the latitude embracing the Chautauqua banding station amounted to 24.6 percent for black ducks, but 34.0 percent (Table 2) for mallards. In both mallards and black ducks, recoveries dropped off below the 34° parallel (south of the mouth of the Arkansas River).

A comparison of the latitudinal distribution of direct and indirect band recoveries is presented (Table 24) for purposes of evaluating the homing of black ducks on migration corridors. For the Lake Chautauqua bandings there was a higher percentage (60.3) of direct recoveries than indirect recoveries (51.2) at the latitude of the banding station.

Table 24. — A comparison of the latitudinal distribution of black duck direct and indirect recoveries, from ducks banded at Lake Chautauqua, 1939–1944 and 1947–1952, for 1 degree north of the banding station to the Gulf of Mexico.

Degree of Latitude	*Percent of Recoveries*	
	Direct	Indirect
41–42	5.0	14.0
40–41[a]	60.3	51.2
39–40	9.5	6.4
38–39	5.6	1.6
37–38	2.2	7.6
36–37	6.1	4.8
35–36	6.7	3.6
34–35	2.8	6.8
33–34	0.6	0.4
32–33	0.6	0.4
31–32	0.0	1.2
30–31	0.0	1.6
29–30	0.6	0.4
Total	*100.0*	*100.0*

[a] Lake Chautauqua.

Direct recoveries were 1.18 times more frequent than indirect recoveries suggesting that only 15 percent of the black ducks failed to return to their "home" latitude. The black ducks that missed their home latitude either spent their allotted migration time in the latitude immediately north of the banding station or farther south, especially between the 34° and 38° parallels.

McGinnis Slough Bandings

(Black ducks are relatively more abundant at McGinnis Slough as a result of its more easterly location, than at Lake Chautauqua. Consequently, 4,887 black ducks were banded there during the fall seasons, 1940–1947, and this number included a large part of the total population. In the fall of 1947 the peak population of black ducks at McGinnis Slough was 1,020. Population estimates were not made in earlier years, but from cursory observation the numbers were believed to have been between 800 and 1,500 at the height of migration.)

Longitudinal Distribution.—Based on 509 indirect band recoveries, the axial line, derived from joining the longitudinal mean for each degree of latitude, does not vary much from straight north and south (Fig. 24). The axial line bisects Lake Superior, jogs to the west, and then resumes a southward direction along the west shore of Lake Michigan. Waterfowl habitat and intensive hunting along the Illinois River pulled the axial line westward from the lower end of Lake Michigan. Then suitable habitat and hunting for black ducks along the Wabash River pulled the axial line back eastward.

South of Illinois, the axial line of recoveries paralleled the Mississippi River, but was from 50 to 75 miles east of it, and a similar distance east of the axial line formed by recoveries of Lake Chautauqua black ducks.

The lines formed by standard deviation of the mean extended over a breadth of 750 miles at the Canadian border. From there south to the site of the banding station, the standard deviation lines converged to a breadth of about 100 miles. The intensive hunting along the upper Illinois River further restricted the latitudinal spread. However, south of central Illinois the longitudinal lines widened again to distances varying from 100 to 350 miles.

The longitudinal distribution of 390 direct recoveries of black ducks banded at McGinnis Slough was similar to that for indirect recoveries (Fig. 24). North of southern Illinois, the distribution of direct and indirect recoveries was almost identical. South of Illinois, standard deviation showed a wider spread in longitudinal distribution for direct than for indirect recoveries. Moreover, the axial line of the direct recoveries in this region averaged about 50 miles nearer to the Mississippi River than that of indirect recoveries.

Latitudinal Distribution. — The latitudinal distribution of indirect recoveries from black ducks (Table 25) showed that almost half of the recoveries occurred at the latitude where the ducks had been banded. However, this was only slightly higher than for wintering mallards returning to the latitude of their banding station north of the Black Hills, South Dakota (Table 18).

It is suggestive that McGinnis Slough banded black ducks returned to spend about half of the open hunting season (within the United States) in the vicinity of their former migratory home. They remained there later during the winter than did mallards, for indirect recoveries of black ducks south of McGinnis Slough amounted to 24.6 percent (Table 25) as compared with 37.9 percent for mallards (Table 7).

A comparison of direct and indirect recoveries for similar latitudes (Table 26) indicates that only 18 percent of the indigenous black ducks failed to return to the latitude of McGinnis Slough. If all had returned, the percentage of direct

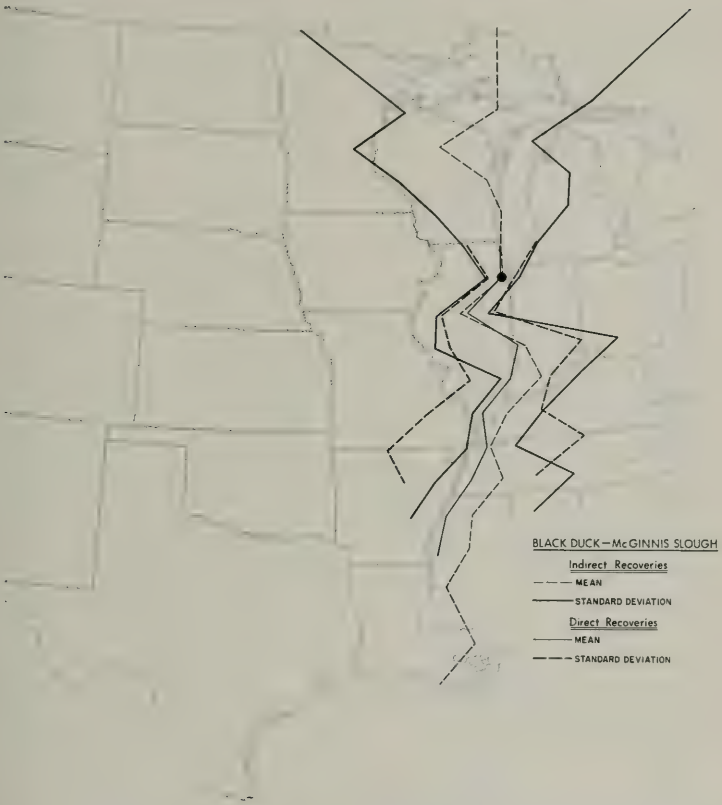

Fig. 24.—The longitudinal distribution of black duck indirect recoveries as compared to direct recoveries on the basis of mean and standard deviation lines. Black ducks banded at McGinnis Slough, Cook County, Illinois, 1940–1947.

and indirect recoveries for the latitude of the banding station (41°–42°) would be the same, inasmuch as local direct recoveries represent the time remaining during the hunting season which the ducks spent in the vicinity of the banding station.

A small proportion of black ducks (as shown by the difference between direct and indirect recoveries) either stopped at the latitude immediately north of the banding station or continued south to other areas, principally between southern Illinois and northern Mississippi.

The direct recoveries show a northward reversal of movement from McGinnis Slough. Nearly all of the black ducks went no farther than 1 degree north (Table 26). Such northward movements may represent birds searching for new feeding grounds, or those that overshot favorite stopping areas and returned.

Table 25. — The latitudinal distribution of indirect black duck recoveries (1941–1952) from autumn bandings at McGinnis Slough, Cook County, Illinois.

Degree of Latitude	*Number of Recoveries*	*Percent of Recoveries*
48–49	3	0.6
47–48	1	0.2
46–47	18	3.5
45–46	22	4.3
44–45	29	5.7
43–44	23	4.5
42–43	34	6.7
41–42[a]	254	49.9
40–41	26	5.1
39–40	12	2.4
38–39	10	2.0
37–38	15	2.9
36–37	13	2.6
35–36	14	2.7
34–35	20	3.9
33–34	4	0.8
32–33	3	0.6
31–32	0	0.0
30–31	5	1.0
29–30	3	0.6
Total	*509*	*100.0*

[a] McGinnis Slough.

Table 26. — A comparison of the latitudinal distribution of black duck direct and indirect recoveries (1941–1952) from 1 degree north of the banding station at McGinnis Slough to the Gulf of Mexico.[a] Ducks banded 1940–1947.

Degree of Latitude	*Percent of Recoveries*	
	Direct	Indirect
42–43	4.5	8.2
41–42[b]	74.7	61.6
40–41	7.6	6.3
39–40	1.0	2.9
38–39	2.1	2.4
37–38	2.4	3.6
36–37	2.6	3.2
35–36	2.9	3.4
34–35	0.8	4.8
33–34	0.5	1.0
32–33	0.0	0.7
31–32	0.3	0.0
30–31	0.3	1.2
29–30	0.3	0.7
Total	*100.0*	*100.0*

[a] Based on 381 direct recoveries and 413 indirect recoveries.
[b] McGinnis Slough.

DISCUSSION

Indirect recovery of mallards banded in Illinois provides a reasonable albeit somewhat distorted presentation of the migration corridor used by these ducks between their breeding and wintering areas. Visual sightings of migrating mallards, radar observations, and weekly waterfowl censuses (1946–1968) disclose that across Iowa the principal course of the mallard population is to the southwest of that shown by band recoveries.

Observation of migration and the relative abundance of mallards on refuge areas along the Mississippi River show that the bulk of these ducks reach this river between Muscatine, Iowa, and Clarksville, Missouri. Band recoveries, on the other hand, show the center of the migration corridor to occur at the Mississippi River farther north, mostly between northern Illinois and southern Minnesota (Fig. 25).

Band recoveries are particularly biased in the region between the Minnesota and Mississippi rivers by the paucity of habitat along the axis of the migration corridor. Yet, there is an extensive mallard habitat in marshes along the Upper Mississippi Refuge which forms the east border of this migration corridor (Bellrose 1968:8). Apparently, the banded ducks migrating along the eastern edge of the corridor come in contact with the Mississippi River farther north (thereby affording more opportunities for shooting and for recovering bands) than do the bulk of the migrants. Thus the band recoveries do not delineate the course taken by most mallards using this particular migration corridor.

A similar situation prevailed for certain Illinois bandings in the eastern North Dakota-western Minnesota region. As previously discussed, the variation in habitat resulted in a migration artifact, a zigzag in the longitudinal distribution of band recoveries.

A third region in which waterfowl

habitat biased the longitudinal distribution of mallard band recoveries was in southern Illinois and Indiana. Because of the high kill of mallards made at Hovey Lake and other areas in southwestern Indiana, compared with that made in southern Illinois, band recoveries in the Hovey Lake area were far out of proportion to known waterfowl abundance in the two areas.

Intensive hunting in the extensive waterfowl habitat along the Mississippi

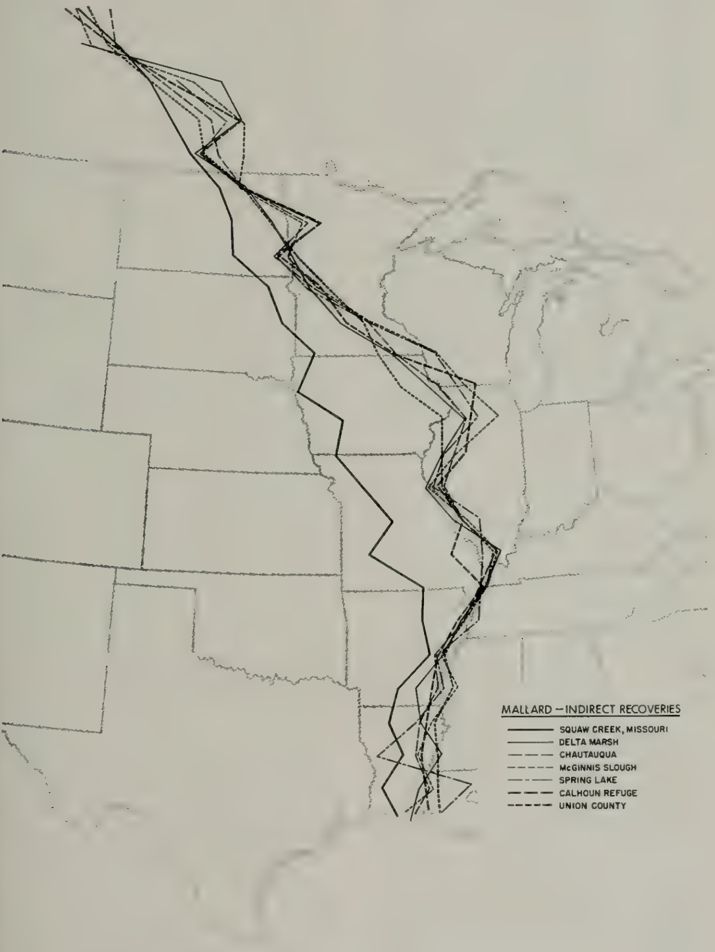

Fig. 25. — A comparison of the mean lines of indirect mallard recoveries from bandings at seven stations in the Mississippi Flyway.

River in Iowa, Illinois, and Missouri pulled the mean line of Squaw Creek indirect recoveries (Fig. 25) to the east of the Missouri River. Visual sightings of mallards in migration indicate that there is a larger passage along the Missouri River valley in western Iowa and Missouri, then eastward as far as the Mississippi migration corridor.

Outside of the above biases in band recoveries resulting from the restricted distribution of waterfowl habitat and hunters, band recoveries appear to adequately delineate the geographic distribution of mallard passage.

Biological Implications

Fig. 25 shows the uniform migration pattern exhibited by mallards banded at five stations in Illinois and at the Delta Marsh, Manitoba. The greatest difference in the mean band recovery lines occurred in the vicinity of each banding station. It is obvious that each banded group tended to break away from the main stream of migration within 100 miles of its respective home lake and take the most expedient direction to its home area. When the group departed from its home lake, the course of flight once again merged with the main stream of migration within 100 miles.

The main stream of mallards migrating to the Midwest arises in central Saskatchewan and assumes a southeasterly course primarily to the Mississippi River, secondarily to the Illinois River, and also to other waterfowl habitats. The main stream, which we have also called the Mississippi migration corridor, turns southward at the Mississippi River, the Illinois River, or some other important water area in the Midwest to reach wintering grounds largely in eastern Arkansas, western Tennessee, western Mississippi, and northern Louisiana.

Mallard bandings at Squaw Creek point to a passage of secondary magnitude from central Saskatchewan. This migration corridor arises from the same general breeding grounds as does the Mississippi migration corridor. However, it proceeds south-southeasterly rather than southeasterly to the Midwest. Because it is associated with the Missouri River, where its separation is greatest, we have termed this the Missouri River corridor (Bellrose 1968:6).

Because bait was used to attract ducks to the banding traps, some biologists have suspected that in subsequent years this attraction might have influenced the return of banded birds to the trap areas. A comparison of the distribution of indirect recoveries for both mallards and black ducks shows no discernible difference in returns to the banding area between those years in which bait was available and years in which it was unavailable. Bait was available in those years for which there were direct band recoveries for Lake Chautauqua, McGinnis Slough, and Spring Lake, Illinois bandings. Bait was unavailable in years in which there were no records of direct recoveries, for then no bandings were made at those stations. Thus, the high rate of indirect band recoveries in the vicinity of the banding station does not occur as a result of the ducks being attracted by bait.

There is increasing documentation on the homing of many species of waterfowl to particular breeding and wintering areas. In ducks, this return to opposite ends of their migration corridors applies especially to individuals having made one round trip. Although there is evidence of yearling ducks returning to their natal areas, the proportion is less than for older birds.

At the Delta Marsh, Manitoba breeding grounds, Sowls (1955:33) retrapped in subsequent years the following percentages of adult hens on their nests: pintail *(Anas acuta)* 39; gadwall *(Anas strepera)* 37; shoveler *(Spatula clypeata)* 42; blue-winged teal *(Anas discors)* 14; and mallard 13. Considering that the annual mortality rate of these species is close to 40 percent, and that the nests of some individuals were overlooked, Sowls concluded that practically all the pintail, gadwall, and shoveler hens alive returned to nest in the same area. Apparently some pioneering to new areas, possibly within a few miles, occurred among mallard and blue-winged teal hens.

Adult wood duck *(Aix sponsa)* hens in Illinois also return to their initial nesting area (Bellrose et al. 1964:671). Almost half of the hens captured on nests one year were captured in the same area the following year. An annual mortality rate of almost 50 percent points up the fact that practically every adult hen wood duck alive homed back to the same nesting area in Illinois.

At least 6.5 percent of the juvenile banded wood ducks returned to nest in the same area where they were reared (Bellrose et al. 1964:672). Banding data suggest that a high mortality occurs among immatures, which may amount to 80 percent the first year. Also many of the returning yearlings would not nest in houses, the principal source of captured birds. Hence, it is most likely that the proportion of returning yearling wood ducks was much greater than that shown by the 6.5 percent return rate.

Of 185 captive-reared juvenile hens among 5 species of ducks released during the summer at Delta Marsh, Sowls (1955:36) reported that 18 (9.7 percent) returned as yearlings. However, pen-reared juvenile ducks are known to suffer exceptionally high mortality in the wild; consequently, probably fewer than 40 of the 185 ducks had survived. As among adults, the mallard and blue-winged teal yearlings showed a lower return to the home area than did pintails, gadwalls, and shovelers.

The precise homing of buffleheads *(Bucephala albeola)* has been described by Erskine (1961:393). Of 20 hens banded on their nests in the central plateau region of British Columbia, 18 were captured in subsequent years on nests at the same lake and 2 on nests at nearby lakes. Two hens were caught in 3 consecutive years on the same nest. Four other hens were banded as young, 3 of which nested in later years at the same lake and 1 on another lake less than 1 mile away.

Mendall (1958:117) believed that in the northeastern United States homing to breeding areas occurred consistently in black ducks, ring-necked ducks *(Aythya collaris)* and wood ducks. He reported that a number of black ducks, banded as juveniles or brood females, were found during subsequent nesting seasons in the same region where they were originally captured. Circumstantial evidence of homing was the finding of several black duck nests at identical sites in succeeding years. Eight ring-necked ducks, 5 juveniles and 3 adult hens returned to nest in the same marsh where they were initially banded.

Lensink (1964) analyzed many thousands of band recoveries from ducks banded as flightless young on their rearing grounds. Band data from a region of about 48,000 square miles in southwestern Saskatchewan provided information from which Lensink (1964:19) concluded:

> ". . . (1) direct and indirect recoveries of both sexes cover essentially identical geographical areas, (2) except for the high incidence of direct recoveries near the banding station, the direct and indirect recoveries from bandings in Saskatchewan have similar distribution patterns, and (3) a highly developed homing tendency is indicated by indirect recoveries that are no more scattered from the area of banding than the direct recoveries of birds banded as locals. The tendency to return to the general region of origin is apparent among males as well as females and does not appear to have been changed by habitat deterioration during drought years."

Lensink's findings were for an extensive region of the breeding grounds, which is not comparable to homing to a specific area, such as a large marsh or a group of potholes. Nevertheless, Lensink's findings show a pronounced return of both yearling drake and hen mallards to the general area of their origin.

Waterfowl are also known to return to specific wintering areas. This is especially evident in Canada geese (Hanson & Smith 1950; Vaught & Kirsch 1966). Ducks home to their wintering grounds too, but it is not as well known. Based on the banding of 17,395 mallards at five stations in British Columbia, Munro (1943:229) reported that they ". . . return to the same wintering grounds on the Coastal Plain [British Columbia] and trap recoveries show that some return to the precise locality."

Lauckhart et al. (1961) tabulated direct and indirect recoveries of mallards banded in the Pacific Northwest. They analyzed indirect recoveries from bandings in eight regions of Washington, Oregon, Idaho, and the northern half of California. For all these banding regions, the largest number of indirect recoveries were from ducks that had returned to the respective locality of each banding station. Mallard populations were transitory in only two (eastern Idaho and northeastern California) of the eight regions where bandings occurred. The other six regions are known to be terminal wintering areas. In these six regions (eastern and western Washington, eastern and western Oregon, southwestern Idaho, central California) fewer than 5 percent of the indirect recoveries occurred south of the respective banding areas. Thus, there is ample evidence of a strong homing by mallards to specific wintering areas in the Pacific Northwest.

Mallard bandings made during the winter in the northern Black Hills of South Dakota (Drewien 1968 and Table 18) show that 22 percent of all recoveries in subsequent years were south of that wintering area. Although the data show an important return to the same wintering area, they also point up that numbers of mallards did migrate farther south in subsequent winters.

Bandings of mallards made at several stations in Illinois also show a north-south variation in wintering locations. The main wintering grounds for these ducks occurs between 34° and 37°. Indirect recoveries in that region from Chautauqua banded mallards varied from 10.5 percent in 1941 to 28.2 percent in 1950. However, in half of the years from 1940 through 1966 the variation between years was no greater than 5 percent.

At the Union County Refuge in southern Illinois, wintering mallards were banded even though the station lies just north of the principal wintering grounds, between the 34° and 37° parallels. In the years following banding at Union County, the proportion of mallard bands from the principal wintering grounds varied from a high of 44.1 percent in 1955 to only 6.8 percent in 1963. In 1963, 9.8 percent of the recoveries, an unusually high number, came from latitudes south of the 34° parallel.

Such variation in the apparent yearly abundance of Illinois banded mallards on their principal wintering grounds points to a flexible homing to specific localities. There is a strong tendency to home, but the north-south distribution is influenced by weather and food conditions. This also applies to the population of mallards wintering in the Black Hills, but, obviously, mallards in the Pacific Northwest behave differently.

Mallards in the Pacific Northwest exhibit a much greater degree of homing to specific wintering grounds than do mallards of the Mississippi migration corridor. Because of maritime influences, winter weather in the Pacific Northwest is more moderate and stable than the unstable Great Plains weather which affects most of the Mississippi migration corridor. Therefore, mallards in the Mississippi migration corridor are definitely more mobile on their wintering grounds than those of the Pacific Northwest. They need to have a flexible homing behavior to meet changing weather and habitat conditions.

On wintering grounds in the Mississippi migration corridor, ice may cover water areas some years and not others; snow may or may not cover grain fields; mast may be abundant or wanting in river swamps; river swamps may be dry in some years and flooded in others. All these conditions affect the availability of the mallard's winter food supply. To meet these conditions on their wintering grounds in the Mississippi migration corridor, mallards often leave one wintering area for other more provident areas. Nevertheless, banding data reviewed here imply that mallards have traditional wintering areas in the Mississippi migration corridor albeit flexible in extent. Banding data presented by Munro (1943:239) and Lauckhart et al. (1961:13–24) indicate that mallards in the Pacific Northwest have more rigid traditional wintering areas.

Black duck bandings analyzed by Addy (1953) show a consistent homing to specific wintering areas along the Atlantic Coast. Coastal banding stations which showed a large proportion of indirect recoveries in their vicinities and only a very small proportion to the south were stations near Newburyport and Cape Cod, Massachusetts; Long Island, New York; Chincoteague and Back Bay, Virginia; and New Holland, North Carolina.

Examples of the degree of homing to Massachusetts and Long Island stations suffice to illustrate this point. For black ducks banded during the winter at Newburyport recoveries in subsequent years amounted to 60 percent of all recoveries within a 50-mile radius of the station (Addy 1953:11). Only 3 percent of all recoveries were from areas south of New England. Bandings of black ducks during the fall at Cape Cod resulted during subsequent falls in a 52-percent recovery within a 50-mile radius of the station. The proportion of recoveries south of Cape Cod was about the same for direct and indirect recoveries, which amounted to only 8 percent from Long Island and south.

Data for black ducks banded on Long Island, New York during the fall showed that 60 percent of all indirect recoveries occurred locally. Only 9 percent of all indirect recoveries were reported south of Long Island.

Black ducks banded in the interior have been largely from the northern part of their fall and spring ranges. Without the modification of weather brought about by maritime influence, snow and ice make most of the northern interior areas untenable for large populations of wintering black ducks. Small numbers may winter, but band recoveries indicate that the bulk of the ducks migrate to more southerly areas.

This situation is exemplified by recoveries from black ducks banded at stations on Lake Chautauqua and McGinnis Slough in Illinois. Indirect recoveries south of these banding areas amounted to an identical 24.6 percent of all recoveries (Tables 23 and 25) for each station. This is a much larger southward recovery than Addy's (1953) findings for Atlantic Coast stations at about the same latitude (Cape Cod and Long Island).

When food is available we find several thousand black ducks wintering at the confluence of the Des Plaines and Kankakee rivers, only about 25 miles southwest of McGinnis Slough. However, when a deep or crusted snow makes waste corn unavailable, most or all of these ducks depart for more favorable areas to the south.

Therefore, we conclude that where weather conditions are sufficiently uniform from year to year as to make wintering food supplies consistently available, black ducks as well as mallards home to the same wintering areas. Where weather conditions during winter vary greatly in their severity, both the black duck and the mallard exhibit varying degrees of site attachment. Where conditions demand a flexible winter site attachment for survival, both mallards and black ducks have evolved such a behavior response.

A similar flexibility in homing may also apply to mallards on the breeding grounds, but adequate documentation of this is lacking. The only suggestion that mallards may sometimes seek new areas for breeding is Sowls' (1955) finding that both adult and yearling mallards showed a lower return to the Delta Marsh, Manitoba area than did several other species of ducks. Lensink's (1964) conclusion on the return of mallard ducklings to their natal region applies to a rather large region rather than a specific locality.

Less well known than the homing of ducks to breeding and wintering areas is their homing along migration routes. As discussed in this paper, mallards and black ducks return to specific localities in migrating from breeding to wintering areas. Even so, between 25 and 50 percent of the mallards and black ducks which stopped at a migration area one year fail to return to the same area the next year.

Most of the ducks that miss returning to the same area pass on to their wintering grounds. Others stop 50–100 miles short or pass 50–100 miles beyond their traditional migration area. Still others stop at marshes east or west of the one they visited the previous year.

Those ducks which fail to return to a traditional migration area but stop at other areas or continue in passage directly to their wintering grounds may do so for several reasons: 1) Individuals which have made a particular area a migration stop may be in a flock of ducks oriented to a different goal; they may be carried along by other, more dominant, members of the flight. 2) A reduction in the availability of food resources results either in continued southward passage or a pioneering in the area for new supplies. 3) Severe winds may cause migrating ducks to drift off course, or, in the case of head winds, retard migration so that birds land prematurely. 4) On dark nights, especially when low cloud decks prevail, waterfowl may pass over their goal without seeing the landscape cues necessary for pilotage.

Banding, radar surveillance, and visual sighting demonstrate that ducks may depart in migration from a particular area in several different directions. Upon departure we often see a shift in individuals and segments of flocks from one flight line to another. On occasion we have observed flocks and segments of flocks undecided as to which directional flight they should affiliate with; indecisively they have swung from one direction to another. Such behavior leads us to believe that at times individuals and even entire flocks are influenced in choice of direction by the action of more dominant groups (Bellrose 1968:13).

Waterfowl censuses and observations made over a 30-year period in the Illinois River valley show that when a reduction in food resources occurs, many ducks leave and populations decline. Ducks arriving one night and failing to find adequate food have often been observed to leave the next night. The influence of food on duck populations is evident in the sharp decline of lesser scaup *(Aythya affinis)* numbers in the Illinois River valley, following the disappearance in 1954 of their principal food, fingernail clams *(Sphaeriidae)* (Mills et al. 1966:18).

Evidence cited earlier in this paper on the yearly course of mallard band recoveries across southern Minnesota and northern Iowa indicated a drift of migrants. This occurred on nights of major mass flights with strong quartering or beam winds. The region where the suspected drift occurred is one devoid of significant landscape features.

Direct band recoveries (Table 5) and visual observations confirm that there are reversed directional movements of mallards and other ducks. We see most of these reversed flights after a large flight has arrived during the previous night; northward flights the following evening are most prevalent when low, heavy clouds blanket the sky the night the ducks arrived.

We interpret these reversed flights of ducks as being made by those flocks which either bypassed or overshot their home lakes. Our observations suggest that at times migrating flocks arrive at the Illinois or Mississippi valleys south of their goal, and they correct for their displacement by turning northward. Other observations indicate that migrating ducks miss their goal under conditions of poor visibility at night. Probably the farther ducks land from their goal, the less their desire to return. Therefore, some of those missing a migration goal continue on to the next goal, which may be either a migration area or a terminal wintering area.

The detailed homing by mallards and black ducks to specific points on the breeding, migration, and wintering grounds leads us to deduce that landscape features are important factors in their navigational system. We have frequently seen migrating ducks change directions upon sight of prominent landscape features (Bellrose 1966:79–81).

Since mallards on the average remain about 28 days at traditional fall migration areas, they have ample time to become acquainted with local landmarks. Direct recoveries show a cruising radius of about 30 miles around each traditional area, enabling the inhabitants to become familiar with a sizable region before moving on to the next traditional area.

Traditional migration and wintering areas are established by juvenile ducks visiting them for the first time in company with adults who return to the areas they visited the year before. Available evidence (Martinson & Hawkins 1968: 684–686) indicates that flocks of mallards are not made up of family units, as is the case with geese. Recoveries of ducks banded as broodmates (op. cit.: 686) have been obtained from widespread areas, evidence that they did not travel together.

If adult and juvenile ducks do not migrate together as a family unit, how do juveniles align themselves with a group of adults which visit a particular series of traditional marshes? We have good reason to believe that most flocks of ducks are composed of both adults and juveniles. Our evidence is strongest for the mallard, a species we have banded and checked in hunters' bags for nearly 20 years. In checking hunters' bags for age composition, we rarely found all one age class. Only early in the fall, when mallard migration was just getting under way, have we found flocks which were entirely adult drakes. The composition of mallard age classes in the bags was quite similar week by week through the hunting season (Bellrose et al. 1961:441). Also both banded juvenile and adult mallards show similar chronologies in their southward passage (Hickey 1951:286).

From the evidence, we conclude that juveniles migrate with older ducks of the same species. We must conjecture on how a particular group of juveniles became associated with a particular group of adults. However, it is well known that adult and juvenile mallards, and, indeed, most other species, collect in large numbers on particular staging areas on the breeding grounds immediately prior to the fall migration.

On the staging areas are birds in all stages of physiological development. As shown by the protracted period of migration from the breeding grounds, some mallards reach a migratory state 2 months in advance of others. It seems reasonable to assume that juvenile and adult mallards in the same physiological condition would begin to associate together. Unknown to us are the behavioral displays that would indicate to the participating individuals the physiological state of other birds. Owen (1968: 623–625) describes some behavioral mechanisms that apparently served to bring blue-winged teal together in groups on staging areas and prepare them for departure in organized flocks.

Since hundreds and sometimes thousands of ducks would be at the same synchrony level of migratory preparedness, chance could well determine which juveniles associated with which adults. Therefore, juveniles from the same brood (associating partly by chance with adults from different migration corridors and wintering grounds) could well migrate in a dispersed manner from the same staging area. The chance association of juveniles with adults homing to diverse migration areas is probably the reason for certain bandings on the breeding grounds showing different geographic patterns between years.

For example, Gollop & Dzubin found a difference in recoveries between the Central and Mississippi Flyways among flightless young mallards banded near Kindersely, Saskatchewan, 1953–1955.[1] In 1953 they reported 2.3 times as many recoveries in the Central as the Mississippi Flyway, in 1954 it was only 1.1 times as many in the Central Flyway, and in 1955, it dropped further to only 0.8 times as many. This variation in the banded samples of young mallards between flyways may have resulted not only from chance association with adults bound for the two flyways, but also there may have been a seasonal difference in the physiological state of the young banded in relation to the adults present.

Because the birds in each group of adults, to which juveniles become attached, utilize their own traditional migration areas, the juveniles are indoctrinated to the same sequence of areas used by their "foster parents." Then those juveniles surviving to the next fall repeat the procedure, returning to the areas they first visited. Only this time, they, as adults, escort juveniles. In this fashion, certain migration and wintering areas become traditional to long-lived individuals. By such an intrinsic form of behavior, a semblance of orderliness is maintained in the pattern of waterfowl migration. Therefore, excessively large numbers of ducks usually do not migrate to habitats of poor quality, nor do good quality habitats usually go unused.

When mallards depart from a particular area in southward migration, they do not all seek the same marsh as their next goal. A large passage from just one staging area is made up of hundreds to thousands of flocks, most of which are bound for diverse localities. However, occasionally we have observed a number of migrating flocks all following an identical path and all bound for the same destination.

An assemblage of flocks obviously migrating along the same route, and with the same goal, is almost as much an entity as individuals comprising a single flock. Because the flocks are usually strung out in a line for miles, we refer to this assemblage of flocks as a "train" flock.

In a light aircraft we have on several occasions followed the track of a train flock. Once we observed flocks of arriving mallards landing at Rice Lake, near Banner, Illinois. Flying in reverse along their line of flight for 90 miles, we passed a flock every 30 seconds to 2 minutes. We found that these migrating flocks were leaving the Skunk River valley 20 miles west of Burlington, Iowa. Some of the flocks were out of sight of each other, yet they were following an identical track east-southeast across the farm lands of Illinois to Rice Lake in the Illinois River valley. Apparently this small population of mallards was migrating as a distinct entity. We believe that they originated from the same water area and followed the same "track" to the same destination. A future challenge is to discover how a train flock originates. How were flocks with the same goal able to assemble at the same place? Banding data presented here show the importance of the old ducks in determining the destinations of flocks from previous visits to a particular area. Therefore, we would conclude that the flocks in a train were brought together by adults with the same migratory pattern. But how did the adults with the same migratory pattern assemble in the same flock?

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[1] From J. B. Gollop & A. Dzubin 1957 mimeographed report with limited distribution, "Waterfowl banding — Whither goest thou?" Report to members of the Mississippi Flyway Technical Committee (now the Technical Committee of the Mississippi Flyway Council).

Such train flock passage usually involves relatively small numbers of mallards, 1,000 to 10,000. When we have observed flights of major proportions, many different goals were involved. One of many observations was reported in a recent paper (Bellrose 1966:80): "Mallards were observed flying parallel to the Illinois River. From time to time we observed flocks from the migrating stream 'peeling off' and landing in one of the many bottomland lakes they were passing. From our knowledge of 'home lakes' provided by band recoveries, I would interpret the peeling off of particular mallard flocks as an indication that they had reached their home lake."

From examining the indirect recoveries of mallards banded at the several locations herein reported, it is apparent that home lakes are dispersed all along the migration corridor. Whereas some flocks may migrate only 100 miles to reach their next home lake, other flocks migrate 200 miles or more, and a few even up to 1,000 miles.

It should be emphasized that among waterfowl migrants, as indeed among all bird migrants, there are three classes of visitants to any specific area—"fallouts," "dropouts," and "homeouts."

The fallouts are birds forced out of the air space by unusually severe weather, such as thunderstorms, snowstorms, sleet, adverse winds, and the like. They are often forced to seek temporary refuge in habitat quite foreign to their normal activities.

The dropouts are birds which have ended their migration after a day or a night flight at such habitats as those with desirable attributes for their resting and feeding. They remain only until the following night or until the weather is favorable for continued migration.

The homeouts are birds which return to a specific area throughout their lives to spend a considerable proportion of their migration period resting and feeding before continuing in migration. We probably have banded no fallout mallards, and only a small proportion of those which are dropouts. The mallards we have banded in Illinois have been largely from those composing the homeout segment of the population.

Management Implications

The analysis of band recoveries reported in this study lends evidence to our belief that ducks migrate along definable areas of geography, smaller than flyways, which we have referred to as "migration corridors" (Bellrose 1968). What sets one migration corridor apart from others is the breadth of passage of a homogeneous segment of a waterfowl population. A homogeneous segment of a population in migration may be defined as flocks of a particular species which exhibit similar geographic and habitat affinities.

Populations of ducks from any premigratory staging area migrate to a sequence of wetland areas within corridors from 150 to 250 miles wide, as shown by standard deviations of band recoveries. Only when mallards are departing or approaching a specific area frequented the year before does the breadth become smaller.

Most species of ducks exhibit a high degree of homing to specific areas on breeding, migration, and wintering grounds, as do Canada geese *(Branta canadensis)*. It would appear, therefore, that ducks should afford the same potential regional manipulation of harvest as do geese. However, there are basic differences in flock organization between ducks and geese which operate against such management.

As discussed earlier, Canada geese migrate as family units, whereas young from the same brood of ducks are likely to disperse among different flocks (Martinson & Hawkins 1968). From many staging areas flocks of ducks may migrate along several different migration corridors. Because of some dispersal of broodmates in migration, a particular breeding area may contribute to several migration corridors, and sometimes to more than one flyway. Moreover, ducks from a specific migration corridor fan out over an extensive part of the breeding range, as illustrated by the distribution of band recoveries in Canada (Fig. 8). On the other hand, it is well known that Canada geese from a particular migration corridor breed in close proximity to each other in well-defined geographic areas.

The geographic fidelity of distinct elements in breeding populations of Canada geese makes it possible to regulate their kill along specific migration corridors. Evidence at present suggests that the kill of ducks along one migration corridor would have some degree of influence, through the breeding population, on the population status of adjacent migration corridors. This stems from the potential dispersal of a brood to more than one migration corridor. Consequently, the available evidence indicates that the duck harvest cannot be regulated on a corridor basis as precisely as it is for Canada geese.

Certain critical information is needed before establishing hunting regulations on the basis of migration corridors rather than flyways. We need to know much more about the degree of dispersal in broodmates along different migration corridors. We need to know the motivation and selection that governs the formation of flocks on premigration staging areas. We need to know, for all important staging areas, the distribution of flocks along the various migration corridors. Until we have much more information on the relationship between various units of breeding populations of ducks and migration corridors, we urge caution in establishing hunting regulations for ducks by migration corridors.

Nevertheless, the fact that there is an affinity among ducks in migration for traditional wetlands provides a new dimension in considering both habitat and population management. Because of a degree of return to specific wetland areas, we see evidence of waterfowl refuges which are overpopulated and others which are underpopulated. We suggest that an example of mallards overpopulating a refuge occurred at the Squaw Creek National Wildlife Refuge up to 1963 and an example of underpopulating a refuge occurs at the Upper Mississippi Wildlife and Fish Refuge. In order to achieve maximum efficiency in a refuge system, it is essential to distribute refuge areas according to the intensity of use along each migration corridor. How well this has been done requires further appraisal, species by species and corridor by corridor.

A population segment indigenous to a particular migration corridor could conceivably be overharvested or underharvested. If consistently overharvested, it could result in migration habitat being occupied below its carrying capacity. This would arise from the fact that fewer adults from that particular corridor would be available to attract their share of juveniles from the gathering of young on premigration staging areas. We are presuming, of course, that chance divides the juvenile ducks on the staging area equally among the available "adult guides," and, moreover, that the staging area is frequented by adults from more than one migration corridor. Potentially, at least, the corridor represented by the largest number of adult guides on the staging area would logically receive the lion's share of available juveniles.

SUMMARY

1. Recoveries from the banding of mallards at five locations in Illinois, at the Delta Marsh, Manitoba, and at the Squaw Creek National Wildlife Refuge, Missouri, were analyzed. Recoveries from black ducks banded at two stations

in Illinois were also compared as to geographic distribution.

2. The geographic distribution of band recoveries was analyzed on the basis of longitude and latitude. Comparisons of the longitudinal distribution in recoveries were made by establishing the mean and its standard deviation for each degree of latitude. Standard deviation implies that two-thirds of the band recoveries for each degree of latitude occurred within the longitudinal deviates.

3. Indirect recoveries from mallards banded at the Delta Marsh, Manitoba, and the McGinnis Slough, Spring Lake, Lake Chautauqua, Calhoun Refuge, and Union County stations in Illinois all showed the same basic geographic pattern. The principal difference in the recovery patterns from these six stations occurred about 100 miles to the north and to the south of each station. In these zones, the recoveries indicated a departure of the mallards from the main stream of passage to return to the area frequented the previous year.

4. The axis of the indirect recoveries from Illinois and Delta Marsh mallard bandings extended southeastward from east-central Saskatchewan to north-central Illinois, and then almost straight south to south-central Louisiana.

5. Indirect recoveries from mallards banded at the Squaw Creek National Wildlife Refuge, Missouri, showed a similar origin to those groups banded at the Delta Marsh and in Illinois. All banded groups of mallards seemed to have commenced their fall migration from east-central Saskatchewan. However, near the United States border, the Squaw Creek banded mallards pursued a more south-southwesterly course than those banded at the Delta Marsh and in Illinois. The east-west separation of these two bandings was greatest at the latitude of the Squaw Creek Refuge. On their principal wintering grounds in east-central Arkansas, Squaw Creek mallards were centered only 25 miles west from those of the other banded groups.

6. There are only slight differences between the longitudinal distribution patterns of direct and indirect recoveries for those latitudes and banding stations where data permit comparison. The principal difference that did occur was in the more limited east-west spread in direct recoveries. The greater spread of the indirect recoveries indicates the proportion of mallards which in years following banding passed east or west of their former migration homes.

7. The homing of mallards back to the same degrees of latitude as where they were initially banded is shown by the large indirect recovery rates at the latitudes of the respective banding stations.

8. An index to the degree of homing to the latitude of the banding station can be obtained by comparing the proportion of direct recoveries with indirect recoveries for those latitudes where both occur. At four stations where such comparisons were possible, the indication was that 50–58 percent of the banded mallards alive returned in subsequent years to the latitudes of their respective banding areas. Others undershot or overshot their former areas, showing up in latitudes immediately north or south of their previous fall migration homes.

9. Direct and indirect recoveries indicated that mallards are most abundant on the wintering grounds between the 34° and 36° parallels in eastern Arkansas and western Mississippi. Thus, mallards banded over an extensive region of the Midwest concentrated in the same general region for wintering.

10. Personnel of the South Dakota Department of Game, Fish, and Parks banded 2,144 mallards during winter in the northern Black Hills. Indirect recoveries at the latitude of the banding station amounted to 46.4 percent of the total, evidence of the large proportion of mallards that returned to their former wintering area.

11. The seasonal turnover in mallard populations during the fall at Lake

Chautauqua was analyzed on the basis of elapsed time in direct recoveries, elapsed time in repeat captures at the banding traps, and the relative proportion of indirect recoveries at any 1 degree of latitude. The proportion of band recoveries was equated with time available during the hunting season. The elapsed time of direct recoveries received from the area of the banding station was 17.3 days for adult drakes, 14.9 days for juvenile drakes, and 16.0 days for hens. Repeats of mallards in the banding traps indicated an elapsed time of 10–11 days. Indirect recoveries indicated that mallards remained in the Lake Chautauqua area for 27.9 days. It is believed that the figure derived from indirect recovery data was the most valid.

12. The chronology of mallard passage down the Mississippi migration corridor was plotted from indirect recoveries. Peaks in recoveries occurred September 20–26 in the Canadian zone, October 25–31 in the northern zone of the United States, November 8–15 in the central zone, and December 27–January 3 in the southern zone. The principal southward passage occurred over a 2-month period, October 15–December 15.

13. Black ducks were banded at McGinnis Slough and Lake Chautauqua locations, respectively, in northern and central Illinois. The black ducks banded in central Illinois commenced their southward passage largely from Ontario west of Lake Superior. Those banded in northern Illinois started their fall flight from that region of Ontario north of Lake Superior. Both groups wintered in the same region, centering around the Mississippi River south of Illinois.

14. The mean and standard deviation lines of black duck recoveries showed that with respect to longitude a large proportion returned to the areas of their banding stations. The east-west spreads in direct and indirect recoveries at the McGinnis Slough banding station were almost identical, indicating that only a few returning ducks stopped at areas east or west of there.

15. The latitudinal distribution of black ducks also showed a high degree of homing. A comparison of the direct and indirect recoveries by latitude indicated that only 15 percent more direct than indirect recoveries occurred at the latitude of Lake Chautauqua for bandings made there and 18 percent more direct than indirect recoveries at the latitude of McGinnis Slough for bandings made there.

16. In several areas of the Mississippi migration corridor the waterfowl habitat is so unevenly distributed that the mallard recoveries are biased geographically. However, in general the indirect recoveries reflected the corridor of passage between the breeding and wintering grounds.

17. The detailed homing by mallards and black ducks to specific areas on breeding, migrating, and wintering grounds points up the importance of landscape features as cues in migration.

18. It appears that traditional migrating and wintering areas become established by juvenile ducks visiting them for the first time in the company of adults who return to the areas they previously frequented.

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rimental area at the Morton Arboretum, Lisle, Illinois. The picture was taken in April 1965

Fertilization of Established Trees:

A Report of Field Studies

Dan Neely
E. B. Himelick
Webster R. Crowley, Jr.

Prior to this study the two senior authors, as plant pathologists, had recommended fertilization as a preventive or corrective control measure for several tree diseases. It was recognized, however, that the procedures for fertilizing established trees had not been thoroughly subjected to scientific evaluation; more experimental data were needed.

While cooperating with the junior author at the Morton Arboretum, Lisle, Illinois, on plant disease studies in 1962 the senior authors learned of an experimental area in the Arboretum which contained uniform, established trees in 100-tree blocks with tree spacing intervals optimum for fertilizer trials. In this area a cooperative study was initiated with the Morton Arboretum.

Following the early successful attempts at measuring growth response to fertilizer applications in 1963 and 1964 at the Morton Arboretum, the senior authors expanded the study with trials at four additional sites in Illinois through 1968.

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REVIEW OF LITERATURE

Application of mineral nutrients to soil to stimulate tree growth has been a subject of discussion by arborists for 40 years or more. Most of the procedures used in tree fertilization have been based on field experiences; few have been based on scientific experimentation.

Forest trees or fruit trees are often used as ornamentals or shade trees. Therefore, experimental results on tree fertilization obtained by foresters and pomologists benefit aborists. A book edited by Childers (1954) reviews the knowledge of mineral nutrients of fruit trees. Since pomologists are mainly interested in fruit production, their experiences are probably not as relevant as those of foresters. Recent symposia at two universities dealt with the mineral nutrition of forest trees—Duke University School of Forestry (1959) and University of Florida (1968). Stoeckeler & Arneman (1960) reviewed the information on fertilizer use in forests. Several hundred papers on forest fertilization research are included in the bibliographies of White & Leaf (1956) and Mustanoja & Leaf (1965). Most forestry fertilizer trials have been conducted in forest nurseries or with evergreen species, not with established deciduous trees.

The number of fertilizer field trials pertinent to the arborist is small. In 1927 and 1928 Jacobs (1929) compared fall application with spring application of fertilizers on American elm and Norway maple street trees. Each species was approximately 5 cm in trunk diameter at a point 1.0–1.2 m above the ground. Jacobs concluded that there was "little difference between fall and spring treatments but a decided benefit from either treatment compared with trees which received no treatment."

Beilmann (1936) also recognized the need for data on the effects of fertilization on shade trees. Although many of his tests did not include control plots, he performed tests on several tree species between 1928 and 1933. He devised a formula for rate of fertilization based on tree height, branch spread, and trunk circumference.

Wyman (1936) reported the results of a well-designed 4-year test on nursery-sized pin oaks. He compared results from two combinations of nutrients on two soil types. His fertilizer treatments began the first growing season following planting. During the first three growing seasons, while the trees were becoming established, tree growth was limited. Wyman reported that the fertilization produced a response in twig growth during the second growing season and a response in trunk diameter growth during the third growing season.

Chadwick (1934, 1937, 1940, 1941) measured the annual response of American elms to four nutrient combinations and three seasons of application from 1932 through 1940. The elms were planted in 1931. The nutrients were nitrogen (N), nitrogen and phosphorus (NP), and nitrogen, phosphorus, and potassium (NPK) combinations. The fertilizer was broadcast on the soil surface. Chadwick (1941) states, "The inconsistency of the data recorded indicate that fertilizer experiments on woody ornamentals out of doors must be of a long-time nature . . . ." His study indicated that fall was as favorable as, or more favorable than, other seasons for application of fertilizers and that NPK or NP combinations of nutrients were more beneficial than N alone.

In a test with established Norway maples approximately 4 cm in trunk diameter at 1.4 m height, Chadwick, Tilford, & Irish (1950) applied NPK mixed with water, air (with an air gun), or peat, on the soil surface and into the soil. They also applied N, P, and K singly and in all possible combinations. Fertilizer treatments were applied in April, 1941 and May, 1947. Growth measurements were made each fall from 1941 through 1948. The results indicated that surface applications of fertilizer resulted in a greater diameter increase than other methods of application and that nitrogen may be considered the limiting element for good growth, but that when nitrogen is coupled with phosphorus a greater stimulation may result.

Other results of tree fertilization field studies in the late 1930's or early 1940's include the report by Chandler (1939) who concluded that heavy applications of nitrogen fertilizers increased twig growth of beech and sugar maple by more than 100 percent. Deuber (1939) found that it was possible to kill young trees by using extremely heavy rates of fertilizer. Pridham (1938), in continued observation of the pin oak plots fertilized by Wyman, stated that after seven growing seasons the untreated trees were as large as the trees fertilized at planting. He stated that variance in growth due to fertilization at time of planting is much less than the variance in growth due to season, soil, time of planting, and method of planting. Pridham was unable to demonstrate a stimulation of trunk diameter growth of large American elms (1940) or red oaks (1941) by fertilization.

Recent reports of tree fertilization field trials include tests on dogwood by Curlin (1962), sweetgum and oak by Broadfoot (1966), tulip tree by Finn & White (1966), and sugar maple and tulip tree by van de Werken & Beavers (1965).

Many nutrients essential to plant growth can enter leaves directly. Pirone (1951) reported results from 3 years of testing foliar applications of nutrients on five species of street trees. He noted that the general appearance of trees receiving six foliar sprays was better than that of untreated trees. His chemical analyses of leaves from a small number of London plane trees and pin oaks showed more nitrogen and phosphorus in leaves from the treated trees than in leaves from untreated trees.

Preliminary data from the tree fertilization field trials at the Morton Arboretum test site reported in detail here were published previously by the authors (1965).

CHARACTERISTICS OF STUDY AREAS

Sites of Fertilizer Plots

The fertilizer trials on deciduous trees (and two species of evergreens) were conducted at five sites in Illinois. The locations of the fertilizer plots are shown on the map of Illinois (Fig. 1).

The site of the original test plot was the Morton Arboretum, Lisle, DuPage County. The Morton Arboretum is a privately endowed educational foundation, founded in 1922 by Joy Morton. The Arboretum is approximately 25 miles west of Chicago.

The second test site was the Illinois Natural History Survey arboretum near Urbana, Champaign County, 1 mile south of the University of Illinois campus. The land is owned by the University of Illinois. It was assigned to the Natural History Survey in 1960.

The third test site was Sinnissippi Forest, a private plantation and naturally forested area along the east bank of the Rock River, 3 miles southeast of Oregon, Ogle County. Although privately owned by Mrs. C. Philip Miller, Sinnissippi Forest is extensively used for scientific purposes and is managed by a University of Illinois resident forester.

The fourth test site was the Lincoln Trail State Park, approximately 3 miles south of Marshall, Clark County. The park is managed by the Illinois Department of Conservation and has a resident

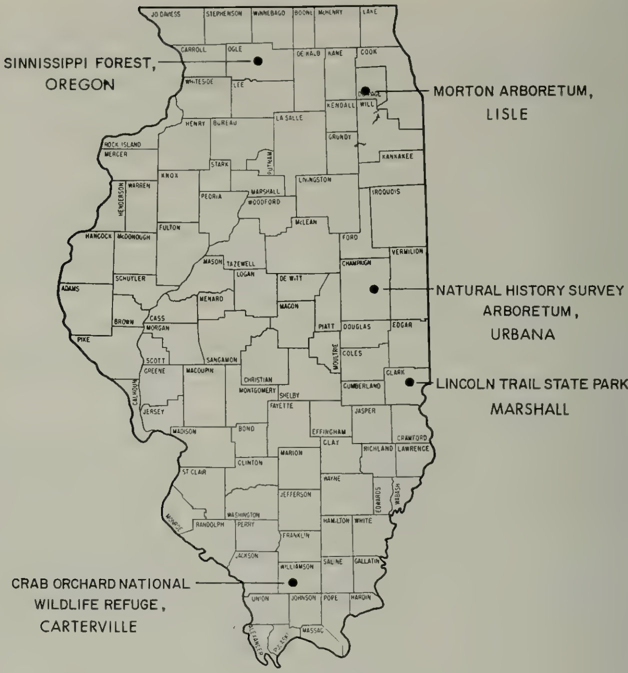

Fig. 1.—The five tree fertilization test sites in Illinois.

ranger. In addition to the natural wooded area surrounding a man-made lake, the park contains numerous deciduous and evergreen tree plantations.

The fifth fertilizer test site was the Crab Orchard National Wildlife Refuge, southeast of Marion, Williamson County. The Refuge is managed by the U.S. Department of the Interior, Fish and Wildlife Service. One of the numerous resident employees is a forester.

Soil Characteristics

In the fertilizer plots in this study at five sites, 10 soil types are represented. The following descriptive information concerning the soil types was primarily obtained from University of Illinois Agricultural Experiment Station Bulletin 725 by Fehrenbacher, Walker, & Wascher (1967).

Loess is the most extensive parent material of Illinois soils. It is a silty material deposited by wind during glacial times. In Illinois, because of the prevailing westerly winds, loess is thickest just east of the sources at the Mississippi and Illinois River Valleys. It thins in a regular manner with distance away from the sources. Glacial drift is also a major source material for Illinois soils. This material was deposited after having been moved by glaciers. The drift deposits are subdivided into glacial outwash, which consists of stratified gravel, sand, silt, or clay deposits, and glacial till, which is unstratified.

Surface soil color is a reasonably good guide to the organic matter content of Illinois soils—the darker the soil the greater the organic matter content. In general, dark-colored soils developed under grass or prairie vegetation and light-colored soils developed under trees or forest vegetation.

The degree of soil development refers to the extent of weathering and change the parent materials have undergone in the formation of the soil. In strongly developed soils the soil profile contains horizons or layers with well differentiated properties of color, texture, and structure.

At the Morton Arboretum the trees in the fertilizer tests were on Andres, Beecher, Markham, and Morley silt loams.

Andres silt loam is a dark-colored grassland soil with moderate development. It formed in silty clay loam glacial till with a mantle of less than 0.5 m of loess or glacial drift. The till is calcareous at 0.5–1.0 m depth. It has a slope of 1–3 percent. The surface soil is a black to very dark brown silt loam 25–40 cm thick with fine crumb to granular structure. The subsurface soil is a very dark brown loam 8–15 cm thick with weak structure. The subsoil is a gray and brown clay loam 30–50 cm thick with imperfect water permeability.

Markham, Morley, and Beecher soils developed from the same parent material as Andres. These, however, are lighter colored, moderately developed soils formed under forest or mixed forest and prairie vegetation.

Markham has a slope of 3–8 percent. The surface soil is a very dark grayish brown silt loam with granular structure 15–20 cm thick. The somewhat lighter colored subsurface soil has weaker structure and is 5–12 cm thick. The subsoil is brown silty clay loam 0.5–1.0 m thick with moderately slow to slow permeability.

Morley has a slope of 4–12 percent. It is quite similar to Markham except that it has a slightly lighter colored and thinner surface soil layer, only 5–12 cm thick, and a thicker subsurface soil layer 8–20 cm thick.

Beecher has a slope of 1–4 percent. It is somewhat poorly drained, since surface runoff is slow to medium and subsoil permeability moderately slow to slow. Otherwise, it is similar to Markham. The surface soil layer is 15–25 cm thick and the subsurface soil layer 8–20 cm thick. There are distinct mottles throughout the subsoil.

At Sinnissippi Forest the fertilizer plots are on Plainfield sand. The Plainfield soils are on nearly level to sloping glacial outwash plains and stream terraces and on sloping to steep morainic areas (2–15 percent slope). They have formed in sandy drift with high quartz and low weatherable mineral content. The soils are excessively drained with surface runoff slow to medium and permeability very rapid. The surface horizon is a dark grayish brown sand 15–25 cm thick and medium acid. The subsoil layer is yellowish brown sand 30–45 cm thick and strongly acid.

The soil in the Natural History Survey aboretum is Flanagan silt loam. It is a dark, moderately developed, grassland soil with a slope of 1–3 percent. It is an imperfectly drained soil that formed in 1.0–1.5 m of loess overlying calcareous loam glacial till. The surface soil is a black to very dark gray silt loam 15–25 cm thick with moderately good structure and medium acidity. The subsurface soil is a dark brown, heavy silt loam 18–30 cm thick. The subsoil is a mottled, brownish, silty clay loam that has moderate permeability and is 75–100 cm thick.

The soil types at Lincoln Trail State Park and Crab Orchard Wildlife Refuge are of similar origin. The four types involved are Stoy, Weir, Bluford, and Wynoose silt loams. All are light-colored, strongly developed soils of southern Illinois that formed under forest vegetation.

Stoy and Weir formed in loess 1–3 m thick on Illinois drift (largely till) or from more than 2 m of loess on bedrock residuum. Stoy has a slope of 1–4 percent. The surface soil is a dark brown friable silt loam with weak crumb structure, strongly acid, and 12–18 cm thick. The subsurface soil is pale brown and 25–35 cm thick. The subsoil is a gray and brown silty clay loam with slow water permeability. Weir has a slope of 0–2 percent. Soil profile depths and colors are similar to those of Stoy. The subsoil contains slightly more clay. Drainage is poor to very poor with runoff slow to medium and permeability slow.

Wynoose and Bluford are very strongly developed soils that formed in 0.5–1.2 m of loess on Illinois glacial drift (largely till) and their subsoil horizons usually extend into the till. Wynoose is quite similar in topography, profile, texture, structure, and reaction to Weir. Bluford is similar to Stoy in these same characteristics.

Data on the available plant nutrient supply as determined by soil tests were obtained from untreated soils from the five test sites. Soil samples collected at the Morton Arboretum from the upper 30 cm of soil and at the Survey arboretum from the upper 15 cm of soil were tested in 1965. Soil samples from the Crab Orchard Refuge, Lincoln Trail State Park, and Sinnissippi Forest plots were collected from the upper 15 cm of soil and tested in 1968. Averages of the soil test data from the tree fertilizer plots are given in Table 1. Additional properties of these soil types are also included in the table.

Precipitation Data

Along with soil fertility, a factor that greatly influences the growth of trees is soil moisture. The precipitation data from the U.S. Weather Bureau collecting stations nearest the fertilizer test sites give an indication of the abundance or sparsity of soil moisture throughout the growing season.

The precipitation data collecting stations were relatively close to the five fertilizer test sites. The collecting stations were located 4 miles northwest of the Morton Arboretum until June 1966 when the station was moved to the Arboretum, 1 mile north of the Survey arboretum, 15 miles east of Sinnissippi Forest, 4 miles northeast of Lincoln Trail State Park, and 4 miles northeast

Table 1. — Soil test data for the soils at the fertilizer test sites.

	Typical Properties[a]			*Soil Tests From Tree Plots*			
Soil Type	Organic Carbon, Percent	Cation Exchange Capacity, m/100 g	Base Saturation, Percent	Number of Samples	pH	P kg/ha	K kg/ha
Andres	...	...	..	15	6.4	18	213
Beecher	3.5	17.2	87	..	...	..	...
Markham	...	...	..	..	...	..	...
Morley	1.1	12.2	..	..	...	..	...
Flanagan	3.0	20.3	73	10	7.0	21	336
Plainfield	0.9	4.0	20	4	5.6	27	129
Wynoose	1.3	9.5	28	5	5.4	9	155
Stoy	1.2	10.4	39	1	5.1	16	222
Weir	0.7	13.6	69	1	5.8	9	113
Bluford	1.8	15.4	17	..	...	..	...

[a] From Fehrenbacher & Odell (1959), Wascher, Veale, & Odell (1962), and unpublished data of Dr. J. B. Fehrenbacher University of Illinois Department of Agronomy.

Table 2. — Precipitation data per quarter year from U.S. Weather Bureau collecting stations nearest the five fertilizer test sites during those years tests were in progress.

Location and Growing Season	*Rainfall, cm* Oct. Nov. Dec.	Jan. Feb. Mar.	Apr. May June	July Aug. Sept.	*Total*
Morton Arboretum					
1962–63	5.8	10.3	26.5	26.2	68.8
1963–64	9.2	10.7	24.9	31.6	76.4
1964–65	10.3	22.6	22.8	43.4	99.1
1965–66	16.7	13.9	35.0	13.4	79.0
1966–67	21.5	12.9	34.7	20.2	89.3
1967–68	23.3	9.9	28.4	36.0	97.6
NHS Arboretum					
1963–64	11.7	19.3	38.9	18.2	88.1
1964–65	13.6	20.6	31.4	45.5	111.1
1965–66	15.4	11.1	27.1	26.9	80.5
Sinnissippi Forest					
1964–65	9.5	14.8	29.0	46.9	100.2
1965–66	19.4	8.4	32.9	13.0	73.7
1966–67	19.8	12.0	31.8	18.3	81.9
1967–68	21.5	5.6	25.7	33.7	86.5
Lincoln Trail					
1965–66	15.0	11.6	28.7	17.5	72.8
1966–67	28.0	19.2	28.3	26.4	101.9
1967–68	40.0	15.5	35.2	26.7	117.4
Crab Orchard					
1965–66	10.6	21.4	44.8	23.0	99.8
1966–67	27.7	17.9	29.1	19.4	94.1
1967–68	36.0	21.5	27.5	17.8	102.8

of the Crab Orchard Wildlife Refuge. The precipitation data at the five test sites for those years in which fertilizer trials were in progress are given in Table 2.

Tree Species and Spacing

Twenty-two species of trees were used in the fertilizer trials in 29 test plots at the five test sites. Twenty were deciduous species and two were evergreen species.

DECIDUOUS TREES

Acer platanoides L.	Norway maple
A. rubrum L.	Red maple
A. saccharum Marsh.	Sugar maple
Carya illinoensis (Wang.) K. Koch	Pecan
Crataegus oxyacantha Pauli' Rehd.	Paul's scarlet hawthorn
Diospyros virginiana L.	Persimmon
Fraxinus americana L.	White ash
F. pennsylvanica var. *subintegerrima* (Vahl.) Fern.	Green ash
Gleditsia triacanthos L. f. *inermis* (L.) Zabel	Honey locust
Juglans nigra L.	Black walnut
Liquidambar styraciflua L.	Sweet gum
Liriodendron tulipifera L.	Tulip tree
Platanus occidentalis L.	Sycamore
Quercus alba L.	White oak
Q. bicolor Willd.	Swamp white oak
Q. rubra L.	Red oak

Q. palustris Muench.	Pin oak
Tilia americana L.	Basswood
T. cordata Mill.	Littleleaf linden
Ulmus parvifolia Jacq.	Chinese elm

EVERGREEN TREES

Pinus resinosa Ait.	Red pine
P. taeda L.	Loblolly pine

Trees in 26 of the 29 test plots were in plantations. Within each plot these

Table 3.—Age, spacing distance, percentage survival, and size of trees in plantations at the five fertilizer test sites, and the type of soil in which the trees were growing.

Site, Test, and Tree Species	*Year of Planting*	*Planting Distance Between Trees, m*	*Planting Survival, Percent*	*Initial[a] Trunk Diameter, cm*	*Soil Type*
Morton Aboretum					
Method					
White ash	1956	4.6 x 6.1	100	7.9	Andres
Honey locust	1957	4.6 x 6.1	66	4.3	"
Pin oak	1956	4.6 x 6.1	100	4.1	"
Time					
Pin oak	1956	4.6 x 6.1	98	5.3	"
Rate					
White ash	1956	4.6 x 6.1	100	8.1	"
Species response					
Basswood	1924	2.4 x 2.4	50	24.6	Beecher
Norway maple	1924	2.4 x 2.4	33	19.5	Markham
Red maple	1924	2.4 x 2.4	67	18.3	"
Sugar maple	1924	2.4 x 2.4	52	17.1	"
Red oak	1926	2.4 x 2.4	60	15.5	Morley
Swamp white oak	1926	2.4 x 2.4	58	12.2	"
White oak	. . . .[b]	±9.0 x 9.0	. .	45.4	Beecher
NHS Arboretum					
Species response					
Green ash	1960	1.5 x 1.8	100	2.6	Flanagan
Chinese elm	1961	1.5 x 2.1	100	2.2	"
Hawthorn	1960	1.5 x 1.8	100	2.3	"
Littleleaf linden	1962	1.5 x 2.1	100	1.3	"
Norway maple	1962	1.5 x 1.8	100	1.7	"
Sinnissippi Forest					
Method					
Green ash	1941	2.4 x 2.4	80	11.2	Plainfield
Red pine	1942	2.1 x 2.1	100	14.1	"
Sycamore	1941	2.4 x 2.4	67	12.2	"
Black walnut	1942	2.4 x 2.4	85	10.6	"
Lincoln Trail					
Method					
Loblolly pine	1951	1.8 x 1.8	86	13.7	Wynoose
Persimmon	. . . .[b]	±3.0 x 3.0	. .	9.3	"
Sweet gum	1951	1.8 x 1.8	75	10.9	"
Sycamore	1951	1.8 x 1.8	68	8.2	"
Tulip tree	1951	1.8 x 1.8	50	10.7	"
Crab Orchard					
Species response					
Pecan	1938	15.3 x 15.3	90	40.6	Weir
Sweet gum	1938	1.2 x 1.2	41	9.7	Stoy
Black walnut	. . . .[b]	±4.0 x 4.0	. .	17.3	Bluford

[a] Average of trunk diameters immediately prior to initial fertilization.
[b] In a natural stand.

trees were of the same age, had a uniform spacing between trees, and within a narrow range had a uniform size. The spacing distances in the different plots varied from 1.2 to 15.3 m (4–50 ft.) between trees. Uniform spacing was a primary factor in selecting test plots and sites; however, in most plots not all the trees originally planted were surviving when the testing began. In three of the test plots, the trees were in naturally regenerated stands. Table 3 lists the tree species used at each of the five sites and gives the planting date, the original spacing between trees, the percentage of tree survival, tree size when testing began, and the soil type.

MATERIALS AND METHODS

In this study the initial tests were aimed specifically at determining what nutrients would stimulate a growth response in established trees when applied in various ways. Sixteen fertilizer treatments were used and each treatment consisted of a different combination of fertilizer and method of application. Later tests were designed to give more limited data that would confirm or fail to confirm the results obtained from the initial tests by utilizing additional species of trees growing in different soil types and locations.

The nutrient elements used in varying amounts and combinations in these tests were the macronutrients nitrogen, phosphorus, and potassium and the micronutrients manganese, iron, copper, zinc, boron, molybdenum, and magnesium. The combinations of nutrient elements were: nitrogen alone (N), phosphorus and potassium (PK), nitrogen, phosphorus and potassium (NPK), and nitrogen, phosphorus, potassium, and micronutrients (NPK+).

Several materials were used as sources of nutrient elements. Ammonium nitrate (33.5-0-0), urea (45-0-0), ammonium sulfate (21-0-0), and ureaform (38-0-0) were used as sources of nitrogen. When the dry form of NPK was needed, a commercial 10-10-10 or 12-12-12 farm fertilizer was used. When an NPK solution was required, a commercial water soluble 23-19-17 fertilizer *(Ra-Pid-Gro*[1]*)* was used. The source materials in *Ra-Pid-Gro* are urea, ammonuim phosphate, potassium phosphate, and potassium nitrate. When P and K were used together in dry form, triple superphosphate (0-45-0) and muriate of potash (0-0-60) were mixed. For the soluble PK treatments, the source material was potassium mono-H phosphate (K_2HPO_4). The combination of micronutrients used was that of *Peters Trace Element Mix*[2], which contains micronutrients as follows (percentages): Mn 9.0, Fe 6.0, Cu 3.0, Zn 3.0, B 2.0, Mo 0.5, and Mg 0.4.

The quantity of nutrient elements per unit area of soil was constant throughout the tests at all five sites regardless of tree size, tree species, tree spacing, or soil type. (The one exception was the rate of nitrogen test on white ash at the Morton Arboretum.) The nitrogen fertilizers were applied at the rate of 29.3 g of elemental N per square meter (6 lb N per 1,000 sq ft). The phosphate fertilizers were applied at 12.9 g of elemental P per square meter (6 lb P_2O_5 per 1,000 sq ft). The potassium fertilizers were applied at 24.3 g of elemental K per square meter (6 lb K_2O per 1,000 sq ft). The amounts of fertilizer source materials used in the soil treatments are given in Table 4.

Foliar fertilization was tested only at the Morton Arboretum. The three water-soluble nutrient sprays applied to the foliage included nitrogen alone, NPK, and NPK plus micronutrients. The amounts of fertilizer source materials used in the foliar treatments are given in Table 5.

Fertilizers were applied to the soil by three methods: (i) broadcast on the soil around the trees, (ii) placed as dry fertilizers into holes made in the soil, and

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[1] Ra-Pid-Gro Corporation, Danville, New York
[2] Robert B. Peters Co., Inc., Allentown, Pennsylvania

Table 4. — Nutrient source materials used to fertilize the soil, and rates of usage at the five fertilizer test sites.

Source Material	*Rate of Usage, g/sq m*	*Elemental Nutrients, g/sq m*
Ammonium nitrate (33.5–0–0)	87.4	29.3 N
Ammonium sulfate (21–0–0)	139.5	29.3 N
Urea (45–0–0)	65.1	29.3 N
Ureaform (38–0–0)	77.1	29.3 N
Triple superphosphate (0–45–0)	65.1	12.9 P
Muriate of potash (0–0–60)	49.9	24.3 K
Potassium mono-H-phosphate	58.6	10.4 P, 26.3 K
Commercial 10–10–10	293.2	29.3 N, 12.9 P, 24.3 K
Commercial 12–12–12	244.3	29.3 N, 12.9 P, 24.3 K
Water soluble 23–19–17	127.6	29.3 N, 10.7 P, 18.0 K
Trace element mix	9.1	0.8 Mn, 0.5 Fe, 0.3 Cu, 0.3 Zn, 0.2 B, 0.1 Mo, 0.1 Mg

Table 5. — Nutrient source materials used in foliar fertilization tests, and rates of usage at the Morton Arboretum.

Source Material	*Rate of Usage, g/1 water*	*Elemental Nutrients, g/1 water*
Ammonium nitrate (33.5–0–0)	4.11	1.38 N
Urea (45–0–0)	3.06	1.38 N
Water soluble 23–19–17	6.00	1.38 N, .50 P, .85 K
Trace element mix	.90	.08 Mn, .05 Fe, .03 Cu, .03 Zn, .02 B, .01 Mo, .01 Mg

(iii) injected as fertilizer solutions into the soil.

In the surface broadcasting method, first the area to be fertilized was measured and the size determined. The fertilizer to be used in this area was weighed and distributed uniformly. In the experimental plots at the Morton Arboretum the trees were spaced far enough apart so that they were treated individually. The treated area around a tree was circular with a radius of 1.7 m (5½ ft) and an area of 9.3 sq m (100 sq ft). The fertilizer was broadcast by hand. In all multiple-tree plots the materials were distributed by machine. The wheeled lawn spreader (Fig. 2) was used at Urbana where the trees were growing in plots that had bluegrass turf. The cyclone type spreader (Fig. 3) was used at all other sites.

Where dry fertilizer was placed in holes in the soil the plots were also measured, their areas determined, and the fertilizer weighed. Holes were either drilled in the soil with an auger and an electric drill (Fig. 4) or formed by punching with a soil profile tube (Fig. 5) or punch bar (Fig. 6). The holes were usually drilled when the soil was dry and punched when the soil was moist. In the single-tree plots in the experimental area at the Morton Arboretum the holes were made in a circular pattern with two circles around each tree and a spacing distance of 0.6 m (2 ft) between holes. In the multiple-tree plots the holes were placed in straight lines with the holes 0.6 m apart in the row and the rows 0.6 m apart. Each hole was 30–40 cm (12–15 in) deep. The volume of fertilizer required for 0.36 sq m (4 sq ft) was placed in each hole using a glass beaker. No effort

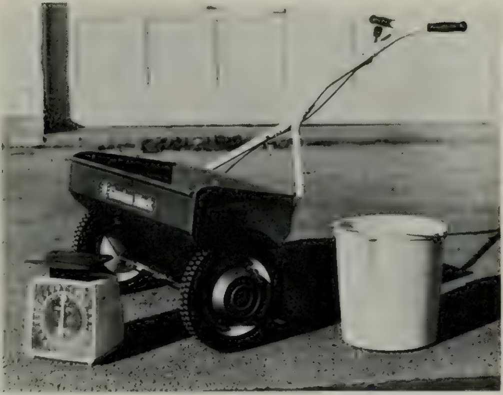

Fig. 2. — The push-type lawn spreader was used to apply bands of fertilizer alongside rows of trees at Urbana.

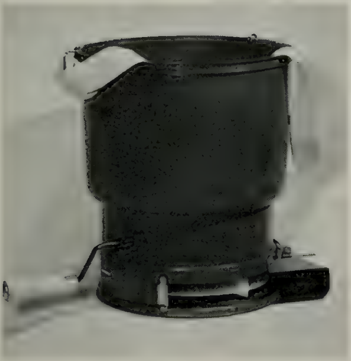

Fig. 3. — The cyclone type lawn spreader was used to apply fertilizer to the soil surface at Lisle, Oregon, Marshall, and Carterville.

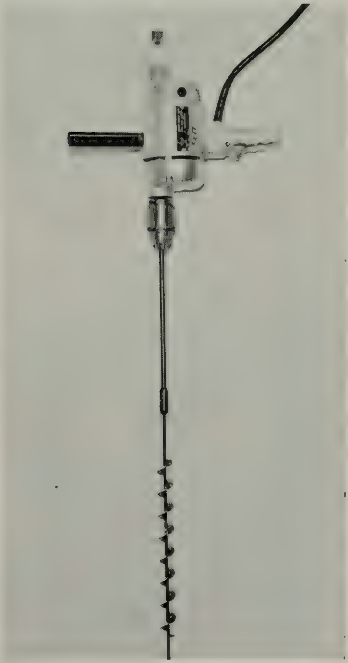

Fig. 4. — The electric drill with a soil auger was used to prepare holes in the soil at Lisle.

was made to fill or close the holes following the distribution of the fertilizer.

Injection of liquid fertilizers into the soil was tested in the single-tree plots at the Morton Arboretum. Enough fertilizer solution to treat 15 trees was prepared. Fifty-seven liters (15 gal) of solution were used per tree with this volume evenly divided into 14 injection sites. It was injected 45–60 cm (18–24 in) deep with a soil needle (Fig. 7) and a

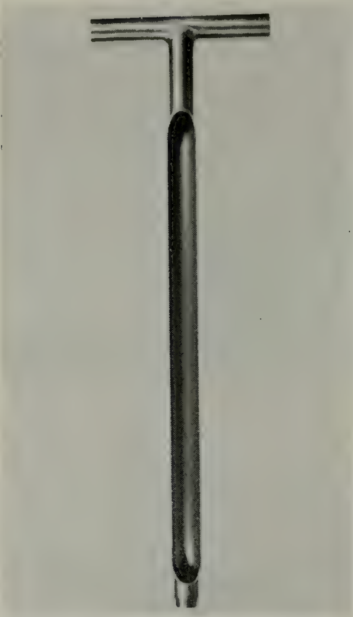

Fig. 5. — The soil profile tube which removes cores of soil from the upper 10–14 inches of soil was used to make holes in the soil at Lisle.

hydraulic sprayer with an agitator using 10 kg per sq cm (150 lb per sq in) pressure. The volume of fertilizer used at each injection site was regulated by opening the soil needle valve for a predetermined number of seconds. Four of the injections were made on the four sides of the tree approximately 0.75 m from the tree trunk and the remaining ten injections were made in a circle approximately 1.4 m from the trunk.

Foliar fertilization was tested on the single-tree plots at the Morton Arboretum. Fertilizer solutions were prepared in amounts to treat 15 trees. The quantities of nutrients applied per tree in foliar treatments were much less than the quantities used in soil applications. The trees were sprayed with a hydraulic sprayer until the solution began to drip from the foliage. No attempt was made to prevent runoff onto the soil. Foliar sprays were applied each year during May, June, and July at approximately monthly intervals. They were applied between 8 A.M. and 12 noon on days having little or no wind. Each tree received 6–8 liters of solution each application.

In all of the fertilizer tests the growth responses were determined by measuring the tree trunks approximately 1 m above the soil. The circumference of each tree was measured with a steel tape at the start of each test and at the end of each growing season. Trees were measured to the nearest 0.005 ft (1.5 mm) in circumference. The height at which the trunk was measured was permanently marked with tree marking paint or with a nail at one or more points around the tree.

The following sections present specific information concerning the different fertilizer tests at the five sites.

Morton Arboretum

With one exception the trees at the Morton Arboretum were in two areas—the experimental area, which is along the northern boundary of the Arboretum and was once pasture, and the forestry plots, which are in the approximate center of the Arboretum and are surrounded by a natural stand of forest trees. The exception was a natural stand of large white oaks immediately adjacent to the experimental area.

The three species growing in the experimental area were pin oak, white ash, and honey locust. They had been planted in square blocks with 4.5 or 6.0 m spacing distances between trees and 7.5 m between blocks. Each block contained 100 trees of a single species. The oaks and ashes were planted in 1956, and the locusts in 1957. When planted, the oaks were 0.3–1.0 m tall, the ashes 1.3–2.0 m tall, and the locusts 1.0–1.3 m tall. All blocks had been

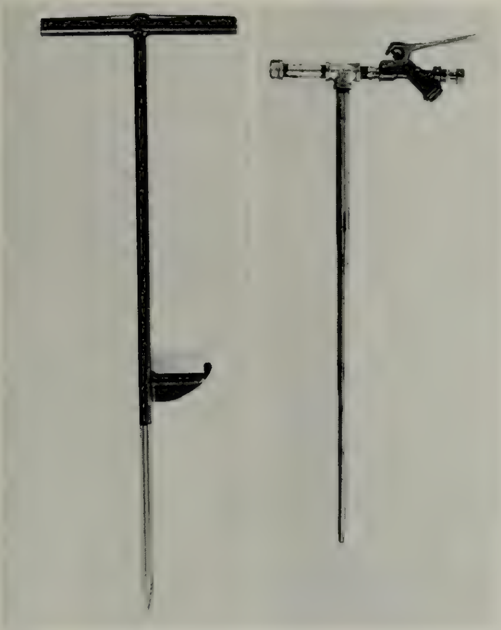

Fig. 6. — A punch bar made from a car axle was used to prepare holes in the soil at Lisle, Oregon, Marshall, and Carterville (left).

Fig. 7. — A soil needle attached to a hydraulic pump with a hose was used to inject water-soluble fertilizers into the soil at Lisle.

planted with Kentucky bluegrass, *Poa pratensis* L., and a sod was maintained with occasional mowing each summer.

White ash, pin oak, and honey locust trees were used in a *method* test. Each block of trees was divided into plots. Each plot contained five contiguous trees and received one of 16 treatments. Eighty trees of each species were treated. Several trees (14 oak, 12 ash, and 10 locust) received no treatment and served as controls.

The 16 treatments included ammonium nitrate and urea each applied dry to the soil on the surface and in holes, in the soil in solution, and as a spray to the tree foliage; NPK and NPK plus micronutrients applied to the soil in holes and in solution and to the tree foilage; and PK applied to the soil in holes and in solution.

The treatment each tree received in 1963 was repeated in 1964 and 1965. Soil treatments were made on May 14, 15, and 16, 1963; on April 22 and 23, 1964; and on April 28 and 29, 1965. Foliage treatments were made on May 6, June 20, and July 23, 1963; on May 20, June 24, and July 24, 1964; and on May 18, June 9, and July 15, 1965.

Annual growth of the trees was measured for 6 years. The initial measurement was made on May 13, 1963 and the subsequent growth measurements were made on October 2, 1963, October 7, 1964, October 14, 1965, September 28, 1966, October 19, 1967, and October 16, 1968.

One block of pin oaks in the experimental area was used in a *time of application* test. Sixteen treatments were used, each treatment applied to five trees selected at random. Ten trees were untreated and served as controls.

In all treatments nitrogen fertilizers were applied to the soil surface. The nitrogen fertilizer source materials were ammonium nitrate, ammonium sulfate, urea, and ureaform. Each tree received 29.3 g of elemental N per square meter (6 lb per 1,000 sq ft) per year. Each source material was applied (i) full rate in April; (ii) ½ rate in April and ½ rate in June; (iii) ⅓ rate in April, ⅓ rate in June, and ⅓ rate in October; or (iv) full rate in October. Each tree received the same treatment for 3 consecutive years; on April 23, June 24, and October 6, 1964; April 27, June 9, and October 14, 1965; and April 26, June 8, and September 27, 1966.

Annual growth was measured for five seasons. The initial tree measurement was made on May 7, 1964 and growth measurements were made on the same days as those reported above for the *method* test.

One block of white ash trees in the experimental area was used in a *rate of application* test. Each tree was treated individually with a random selection for treatment throughout the block. There were 16 treatments with each treatment applied to five trees. Fifteen trees were untreated and served as controls.

All treatments were nitrogen fertilizers applied to the soil surface. The nitrogen source materials were ammonium nitrate, ammonium sulfate, urea, and ureaform. The rates of application were ½, 1, 1½, and 2 times the rates shown in Table 4. Fertilizers were applied on April 22, 1964 and April 27, 1965, each tree receiving the same treatment for 2 consecutive years.

Annual growth was measured for 4 years. The initial trunk measurements were made on April 22, 1964 and subsequent measurements were made on October 7, 1964, October 14, 1965, September 28, 1966, and October 19, 1967.

The remaining fertilizer test at the Morton Arboretum was the *species response* test. The trees in this test (with the exception of the white oaks) were in the forestry plots. They were crowded, relatively small, 40-year-old trees. Relatively uniform groups of approximately 20 trees of each of six species were selected for the test.

Table 6. — Tree species, fertilizer treatments, and fertilizer amounts used per year in species response tests at the Morton Arboretum.

Tree Species	*Treatment*[a]	*Number Trees in Plot*	*Plot Dimensions, m*	*Plot Area, sq m*	*Amount of Fertilizer Used, kg*
Basswood	N surface	9	14.6 x 12.2	178	15.6
	None	9			
Norway maple	N surface	10	22.0 x 9.8	216	18.8
	None	10			
Red maple	N surface	10	14.6 x 9.8	143	12.5
	None	11			
Sugar maple	N surface	11	20.1 x 7.3	147	12.8
	None	11			
Red oak	N surface	10	14.6 x 12.2	178	15.6
	None	12			
Swamp white oak	N surface	12	19.5 x 12.2	240	20.8
	None	11			
White oak	N surface	12	30.5 x 29.4	897	78.4
	None	11			

[a] Ammonium nitrate.

The area was divided into two plots. Ammonium nitrate was broadcast over the soil surface of one plot. The other plot served as an unfertilized control. Plot sizes and fertilizer amounts are given in Table 6. The trees were treated for 3 consecutive years, on April 20, 1964, April 27, 1965, and April 26, 1966.

Initial tree measurements were made on April 20, 1964 and annual growth measurements were made on October 7, 1964, October 14, 1965, September 28, 1966, and October 10, 1967.

Natural History Survey Arboretum

The test in the Natural History Survey arboretum was a *species response* test in a field that had previously been cultivated. The trees were planted, in nursery-type rows, 2 or 3 years before the test began and were just becoming established. A lawn-type bluegrass sod was present.

Ammonium nitrate was applied in 0.6-m wide bands to the soil surface along each side of rows of five species of trees. Alternating 5-tree plots in a row were treated or left untreated with one border tree between plots. No adjacent rows were treated. The trees were treated for 3 consecutive years, on April 16, 1964, May 13, 1965, and May 10, 1966. The amounts of fertilizer applied are given in Table 7. Initial tree measurements were made on May 8, 1964, and the growth measurements were taken on October 12, 1964, October 5, 1965, and October 5, 1966.

Sinnissippi Forest

At Sinnissippi Forest the test plots were in plantations established in open fields that once were farmed. The green ash and sycamore plots were in experimental plantations of approximately 0.4 hectare (1 acre). The red pine and black walnut were in larger plantations. In the ash and pine plantations shading restricted the growth of competing vegetation. Weeds were present in the sycamore and walnut plantations. Each species was divided plots of 10–12 trees with one, two, or more rows of trees separating the plots.

This *method* test compared (i) nitrogen on the surface, (ii) NPK on the surface, (iii) NPK in soil holes, and (iv) no treatment. The ashes received an additional treatment of PK on the surface. The fertilizer treatments and the amounts applied are given in Table 8. The plots were treated on May 5 and 6, 1965, April 28, 1966, and April 18, 1967.

Initial tree measurements were made

Table 7.—Tree species, fertilizer treatments, and fertilizer amounts used per year in species response tests at the Natural History Survey arboretum.

Tree Species	*Treatment*[a]	*Number Trees in Plot*	*Plot Dimensions, m*	*Plot Area, sq m*	*Amount of Fertilizer Used, kg*
Green ash	N surface	8	16.8 x 1.2	20	1.8
	None	9			
Chinese elm	N surface	14	24.4 x 1.2	29	2.6
	None	10			
Hawthorn	N surface	14	24.4 x 1.2	29	2.6
	None	11			
Littleleaf linden	N surface	12	24.4 x 1.2	29	2.6
	None	9			
Norway maple	N surface	20	32.0 x 1.2	38	3.4
	None	19			

[a] Ammonium nitrate.

Table 8.—Tree species, fertilizer treatments, and fertilizer amounts used per year in method tests at Sinnissippi Forest.

Tree Species	Treatment	Source Material	Number Trees in Plot	Plot Dimensions, m	Plot Area, sq m	Amount of Fertilizer Used, kg
Green ash	N surface	Ammonium nitrate	10	12.2 x 9.8	120	10.5
	PK surface	Potassium phosphate	9	17.1 x 9.8	168	9.8
	NPK surface	12–12–12	10	14.6 x 9.8	143	34.9
	NPK holes	12–12–12	10	12.2 x 9.8	120	29.3
	None		12			
Red pine	N surface	Ammonium nitrate	12	10.4 x 8.5	88	7.7
	NPK surface	12–12–12	12	10.4 x 8.5	88	21.5
	NPK holes	12–12–12	12	10.4 x 8.5	88	21.5
	None		12			
Sycamore	N surface	Ammonium nitrate	10	14.6 x 9.8	143	12.5
	NPK surface	12–12–12	10	14.6 x 9.8	143	34.9
	NPK holes	12–12–12	10	12.2 x 9.8	120	29.3
	None		11			
Black walnut	N surface	Ammonium nitrate	11	12.2 x 9.8	120	10.5
	NPK surface	12–12–12	10	12.2 x 8.5	104	25.4
	NPK holes	12–12–12	10	14.6 x 7.6	111	27.1
	None		10			

on May 6, 1965 and subsequent growth measurements were made on September 17, 1965, September 15, 1966, October 20, 1967, and October 10, 1968.

Lincoln Trail State Park

The *method* test at Lincoln Trail State Park was similar in scope and design to that at Sinnissippi Forest. The sweet

Table 9.—Tree species, fertilizer treatments, and fertilizer amounts used per year in method tests at Lincoln Trail State Park.

Tree Species	Treatment	Source Material	Number Trees in Plot	Plot Dimensions, m	Plot Area, sq m	Amount of Fertilizer Used, kg
Loblolly pine	N surface	Urea	7	9.2 x 7.3	67	4.4
	NPK surface	12–12–12	6	17.4 x 3.7	64	15.6
	None		6			
Persimmon	N surface	Urea	8	11.0 x 5.5	61	4.0
	NPK surface	12–12–12	7	14.0 x 5.2	73	17.8
	None		8			
Sweet gum	N surface	Urea	12	10.1 x 9.2	93	6.1
	NPK surface	12–12–12	12	9.2 x 8.2	75	18.3
	NPK holes	12–12–12	12	9.2 x 8.2	75	18.3
	None		13			
Sycamore	N surface	Urea	7	17.4 x 5.5	96	6.2
	NPK surface	12–12–12	8	19.2 x 3.7	71	17.3
	NPK holes	12–12–12	7	10.7 x 7.3	78	19.1
	None		8			
Tulip tree	N surface	Urea	10	12.8 x 8.2	105	6.8
	NPK surface	12–12–12	10	11.0 x 11.0	121	29.6
	NPK holes	12–12–12	10	20.1 x 3.7	74	18.1
	None		9			

Table 10.—Tree species, fertilizer treatments, and fertilizer amounts used per year in species response tests at Crab Orchard National Wildlife Refuge.

Tree Species	*Treatment*	*Source Material*	*Number Trees in Plot*	*Plot Dimensions, m*	*Plot Area, sq m*	*Amount of Fertilizer Used, kg*
Sweet gum	N surface	Urea	19	11.0 x 6.4	70	4.6
	NPK surface	12–12–12	21	11.0 x 9.1	100	24.4
	NPK holes	12–12–12	17	11.0 x 7.3	80	19.5
	None		21			
Pecan	N surface	Urea	1[a]	9.6 x 9.6	92	6.0
	NPK surface	12–12–12	1[a]	9.6 x 9.6	92	22.5
	None		1[a]			
Black Walnut	N surface	Urea	11	23.8 x 11.9	283	18.4
	NPK surface	12–12–12	15	23.8 x 11.9	283	69.0
	None		12			

[a] 10 single tree plots used.

gum, sycamore, tulip tree, and loblolly pine trees were in approximately 0.1-hectare (¼ acre) plantations. The persimmon trees were in a natural stand. Weeds were present in all plots at Lincoln Trail. The treatments and fertilizer amounts used are given in Table 9. The trees were treated on April 21, 1966, April 12, 1967, and March 28, 1968.

Initial tree measurements were made April 21, 1966 and subsequent measurements were made on September 2, 1966, October 10, 1967, and September 26, 1968.

Crab Orchard Wildlife Refuge

The tree plots at Crab Orchard Refuge, with the exception of the pecans, were less uniform than the tree plots at the other four sites. The pecan trees were widely separated in an orchard and were treated as single-tree plots. The sweet gums were in a very closely spaced plantation. Many weakened and dead trees were cut off at the ground line and removed from the plots at the time of the first treatment. The walnut trees were in a natural stand of approximately 0.4 hectare (1 acre). Sugar maples that were competing with the walnuts were killed with 2,4,5-T in 1966. The treatments and fertilizer amounts used at Crab Orchard Refuge are given in Table 10.

The sweet gums and pecans were treated on April 12 and 13, in 1966 and 1967, and April 3 and 4 in 1968. They were first measured on April 13, 1966. The walnuts were treated on April 18, 1967 and April 4, 1968 and were first measured on April 18, 1967. The growth measurements were made on September 2, 1966, September 6, 1967, and September 19, 1968.

RESULTS

The responses to fertilizer applications in this study were measured through comparisons of the annual trunk growth of each tree. The annual growth was calculated from circumference measurements of the trees usually made during the month of October.

Morton Arboretum

The responses to fertilization of pin oak, white ash, and honey locust in the experimental area of the Morton Arboretum were consistent and significant throughout the study. As with all biological data, there were variations between trees, plots, treatments, species, and years during the testing period.

The annual growth determinations in the *method* test are given in tabular form—the pin oak data in Table 11, the white ash data in Table 12, and the

Table 11. — Trunk diameter growth of pin oaks in the method-of-application fertilizer plot at the Morton Arboretum. Five trees per treatment were fertilized in 1963, 1964, and 1965.

Plot	*Nutrient*	*Method of Application*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*					
				1963	1964	1965	1966	1967	1968
1	N[a]	Soil surface	3.70	1.23	1.51	2.14	1.34	1.25	1.24
2	N[a]	Soil holes	4.28	1.31	1.68	2.18	1.28	1.38	1.02
3	N[a]	Soil solution	4.18	1.41	1.67	2.05	1.15	1.22	1.01
4	N[a]	Foliar	4.68	0.89	1.31	1.71	1.12	1.34	0.95
5	N[b]	Soil surface	3.99	1.25	1.60	1.92	1.11	1.19	0.87
6	N[b]	Soil holes	4.72	1.27	1.71	1.89	1.42	1.47	1.18
7	N[b]	Soil solution	4.22	1.17	1.48	1.95	1.14	1.53	1.20
8	N[b]	Foliar	3.76	0.90	1.13	1.27	0.94	1.29	1.25
9	PK	Soil holes	4.27	0.88	1.14	1.18	0.97	1.43	1.19
10	PK	Soil solution	3.85	0.87	1.09	1.24	0.98	1.24	1.04
11	NPK	Soil holes	3.63	1.06	1.56	1.84	1.16	1.42	1.02
12	NPK	Soil solution	3.74	1.61	1.97	2.31	1.33	1.34	1.28
13	NPK	Foliar	4.35	0.80	1.18	1.62	1.10	1.42	1.22
14	NPK+[c]	Soil holes	4.42	1.04	1.94	2.24	1.50	1.60	1.43
15	NPK+[c]	Soil solution	3.78	1.23	1.61	2.06	1.13	1.13	0.90
16	NPK+[c]	Foliar	3.70	0.67	1.16	1.51	0.98	1.40	1.48
Check	None	....	3.76	0.81	1.14	1.29	1.07	1.31	1.24

[a] Ammonium nitrate.
[b] Urea.
[c] NPK + micronutrient mixture.

Table 12. — Trunk diameter growth of white ashes in the method-of-application fertilizer plot at the Morton Arboretum. Five trees per treatment were fertilized in 1963, 1964, and 1965.

Plot	*Nutrient*	*Method of Application*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*					
				1963	1964	1965	1966	1967	1968
1	N[a]	Soil surface	9.82	1.28	1.25	1.56	1.19	1.13	0.92
2	N[a]	Soil holes	8.43	0.89	1.15	1.41	1.13	1.08	0.74
3	N[a]	Soil solution	7.02	0.98	1.04	1.22	0.91	0.74	0.63
4	N[a]	Foliar	8.26	1.01	0.83	0.85	0.95	0.96	0.75
5	N[b]	Soil surface	7.21	0.92	1.05	1.02	1.01	0.76	0.72
6	N[b]	Soil holes	7.75	1.00	1.07	1.42	1.18	1.10	0.79
7	N[b]	Soil solution	7.00	1.26	1.39	1.69	1.38	1.26	1.03
8	N[b]	Foliar	7.37	1.05	0.87	1.16	1.15	1.27	0.91
9	PK	Soil holes	7.62	0.80	0.81	0.87	0.92	0.95	0.79
10	PK	Soil solution	6.80	0.69	0.68	0.87	0.79	0.87	0.76
11	NPK	Soil holes	8.62	1.05	1.06	1.36	1.01	1.05	0.85
12	NPK	Soil solution	7.95	1.23	1.36	1.54	1.21	1.01	0.84
13	NPK	Foliar	7.48	0.78	0.68	0.93	0.91	0.81	0.63
14	NPK+[c]	Soil holes	8.20	0.94	1.13	1.28	1.20	1.06	0.90
15	NPK+[c]	Soil solution	8.57	1.06	1.17	1.36	1.19	1.17	0.69
16	NPK+[c]	Foliar	8.06	0.94	1.00	1.40	1.23	1.32	0.93
Check	None	....	8.06	0.85	0.76	0.92	0.97	1.00	0.88

[a] Ammonium nitrate.
[b] Urea.
[c] NPK + micronutrient mixture.

honey locust data in Table 13. A more condensed and digested version of the data from the 3 species is presented in Table 14, showing the percentage increases of treated over untreated trees.

RESPONSE TO METHOD OF APPLICATION.—Nutrients applied to the foliage of trees stimulated growth much less than soil-applied nutrients. Trees receiving foliar applications grew slightly more or no more than the trees receiving no treatment. The oak and ash trees that received foliar nutrients grew more than untreated trees, while the treated honey locusts grew less than untreated trees (Table 14). The differences in growth between untreated trees and foliar-treated trees were probably due to plot variability rather than treatment response. Statistically, the results from foliar treatments were not significantly better than the results from no treatment (Himelick, Neely, & Crowley 1965). Stimulation of growth, if present, may have resulted, in part, from the uptake of nutrients that dripped from the foliage onto the soil.

All methods of applying fertilizer to the soil stimulated tree growth. Neither surface application, dry fertilizer in soil holes, nor injection of soluble fertilizers into the soil was significantly better than any other soil application method, while all three produced significantly better growth than occurred with foliar fertilization and in untreated controls. Minor variations in growth response did occur between the three soil methods of fertilization. During the 3 years fertilizers were applied, the locusts responded best to surface applications, and the oaks and ashes responded best to solution injection (Table 14). The method of placing dry fertilizers in soil holes was slightly less effective than the other soil methods. Trees treated in this manner, however, tended to show more of a residual response the year following treatment than trees fertilized by surface application or solution injection.

RESPONSE TO NUTRIENTS.—In this test on oak, ash, and locust trees, there was no positive growth response to fertilization with phosphorus and potas-

Table 13.—Trunk diameter growth of honey locusts in the method-of-application fertilizer plot at the Morton Arboretum. Five trees per treatment were fertilized in 1963, 1964, and 1965.

Plot	Nutrient	Method of Application	Average Initial Diameter, cm	Trunk Diameter Growth, cm					
				1963	1964	1965	1966	1967	1968
1	N[a]	Soil surface	5.01	1.35	1.61	1.65	1.23	1.35	1.33
2	N[a]	Soil holes	4.06	0.78	1.13	1.46	1.00	1.32	0.99
3	N[a]	Soil solution	4.26	1.19	1.71	1.92	1.50	1.86	1.81
4	N[a]	Foliar	3.86	0.61	0.54	0.88	0.77	1.11	0.98
5	N[b]	Soil surface	4.19	1.24	1.44	1.64	0.97	1.11	1.15
6	N[b]	Soil holes	3.64	0.63	0.94	1.33	0.98	0.90	0.75
7	N[b]	Soil solution	4.17	1.08	1.33	1.72	1.01	1.04	0.83
8	N[b]	Foliar	3.12	0.54	0.53	0.79	0.59	0.78	0.63
9	PK	Soil holes	4.58	0.55	0.65	0.76	0.71	0.89	0.83
10	PK	Soil solution	4.89	0.58	0.53	0.83	0.71	0.96	0.76
11	NPK	Soil holes	3.91	0.77	0.92	1.34	0.78	0.86	0.77
12	NPK	Soil solution	3.79	0.83	0.99	1.33	0.86	0.95	0.91
13	NPK	Foliar	3.87	0.50	0.52	0.72	0.72	0.87	0.86
14	NPK+[c]	Soil holes	4.62	0.72	0.97	1.28	0.92	0.93	0.80
15	NPK+[c]	Soil solution	5.39	1.03	1.15	1.41	0.93	1.12	1.06
16	NPK+[c]	Foliar	4.82	0.54	0.50	0.61	0.75	1.20	1.00
Check	None	....	5.02	0.66	0.64	0.92	0.86	1.10	1.08

[a] Ammonium nitrate.
[b] Urea.
[c] NPK + micronutrient mixture.

Table 14. — Percent annual trunk diameter growth increase of treated trees over that of untreated trees in the method-of-application fertilizer plots in the Morton Arboretum. Trees were fertilized in 1963, 1964, and 1965.

		Percent Growth Increase Over Untreated Trees								
		Method of Application				Nutrients				
Species	*Year*	Surface	Holes	Solution	Foliar	N[a]	N[b]	PK	NPK	NPK+[c]
Oak	1963	53	44	68	1	63	52	9	64	41
	1964	37	51	47	5	42	40	—2	55	56
	1965	57	58	62	19	64	49	—6	61	67
	1966	15	25	11	—3	18	14	—8	17	23
	1967	—7	12	0	4	—2	7	2	5	4
	1968	—15	—6	—11	—1	—12	—13	—10	—7	—6
Ash	1963	29	14	33	12	24	25	—12	34	18
	1964	51	45	63	12	51	54	—1	59	51
	1965	40	49	58	18	52	50	—5	58	43
	1966	13	16	21	9	11	23	—11	14	24
	1967	—5	7	7	9	—2	4	—9	8	12
	1968	—7	—7	—9	—8	—14	—3	—11	—3	—9
Locust	1963	97	11	56	—17	68	48	—14	21	33
	1964	139	55	103	—19	131	94	—8	50	66
	1965	79	47	74	—18	83	70	—13	46	47
	1966	28	7	26	—17	44	15	—17	—5	8
	1967	12	—9	13	—10	37	—7	—15	—16	—6
	1968	15	—23	6	—19	28	—16	—26	—22	—14

[a] Ammonium nitrate.
[b] Urea.
[c] NPK + micronutrient mixture.

sium (PK). Trees treated with PK alone grew less in almost every instance than untreated trees. Retarding of growth by 5–15 percent was common (Table 14).

The addition of PK to nitrogen fertilizers neither significantly stimulated growth nor retarded growth when compared with the results of applications of nitrogen alone. There was some variation between plots of the three species. During 1963, 1964, and 1965, oaks treated with NPK grew more than those treated with N, whereas locusts treated with NPK grew less than those treated with N. Ashes treated with NPK and N grew approximately the same amount (Table 14).

The oak, ash, and locust trees did not respond to applications of the micronutrient mixture. Of the 27 paired comparisons that can be made from 1963, 1964, and 1965 data in Tables 11, 12, and 13 between plots that received micronutrients and plots that did not, the trees in 10 plots grew more with micronutrients while in the remaining 17 plots the trees grew more without micronutrients.

Nitrogen was the only nutrient that stimulated growth of trees in almost every instance when it was applied to the soil. Nitrogen alone or nitrogen with other nutrients gave approximately the same growth response. During the 3 years the trees were fertilized, the nitrogen source materials stimulated 52 percent increased growth on pin oak, 43 percent on white ash, and 82 percent on honey locust trees.

Pin oaks grew more in 1964 than in 1963 and more in 1965 than in 1964 (Table 11). This increased growth occurred in both treated and untreated trees. The percentages of increased growth of treated over untreated trees, however, do not show this regular pattern (Table 14). This indicates that the increased growth in 1964 and 1965 was due to climatic factors and not to residual nutrients remaining available from treatments in previous years.

Increased growth of the fertilized trees persisted for only 1 or 2 years after fertilization ceased. In 1968, the third year after fertilization ceased, the treated trees grew less than the untreated trees (Table 14). Competition for light, water, or nutrients between trees in the fertilized plots may have limited the growth in 1967 and 1968. The branches between trees in many of the fertilized plots began to touch in 1967, and this was not true in the untreated plots.

RESPONSE TO TIME OF APPLICATION. —Data for comparing the effect of fertilizing trees during different seasons of the year were derived from one block of pin oaks treated with surface application of four nitrogen fertilizers. The annual growth measurements of trees treated at the various seasons are given in Table 15. A summary of this data expressed as percentage increases in growth of treated over untreated trees is given in Table 16.

The greatest growth stimulation was obtained by applying all of the nitrogen in April. Trees receiving a portion or all of the nitrogen in June or October grew less than trees receiving all of the nitrogen in April. Trees fertilized in October grew more than untreated trees.

Unfortunately, the trees treated in October were at a disadvantage in two ways. They were not fertilized in October of 1963; therefore, all fertilizers were not available during the same growing seasons. Also, the fertilized pin oaks were competing for space during 1966 and this factor may have limited the increased response to fertilizers during 1966 and subsequent years. Trees fertilized in April and June responded well to fertilizers in 1964 and 1965, while trees fertilized in October responded well only in 1965 (Table 16).

RESPONSE TO RATE OF APPLICATION. —Data for comparing the response to varying rates of application of nitrogen fertilizers were obtained from one block of white ash trees treated with surface applications of four nitrogen fertilizers. The growth measurements of the trees are given in Table 17.

Data from this test, although more variable than data from previously dis-

Table 15. — Trunk diameter growth of pin oaks in the time-of-application fertilizer plot at the Morton Arboretum. Five trees per treatment were fertilized in 1964, 1965, and 1966.

Plot	*Season of Application*	*Nitrogen Source*	*Rate of N Each Application, g/sq m*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*				
					1964	1965	1966	1967	1968
1	April	N[a]	29.3	4.97	1.34	1.81	1.41	1.44	1.38
2	"	N[b]	29.3	5.37	1.74	2.11	1.48	1.48	1.32
3	"	N[c]	29.3	6.14	1.55	2.13	1.35	1.40	1.32
4	"	N[d]	29.3	5.57	0.97	1.66	1.40	1.55	1.63
5	April, June	N[a]	14.7	5.03	1.24	2.10	1.66	1.34	1.36
6	"	N[b]	14.7	5.85	1.28	1.93	1.59	1.54	1.37
7	"	N[c]	14.7	5.67	1.07	1.63	1.31	1.30	1.09
8	"	N[d]	14.7	5.12	0.95	1.53	1.31	1.30	1.22
9	April, June, Oct.	N[a]	9.8	4.92	1.04	1.61	1.26	1.27	1.15
10	"	N[b]	9.8	5.63	1.29	2.13	1.45	1.66	1.45
11	"	N[c]	9.8	5.18	1.18	1.86	1.43	1.51	1.47
12	"	N[d]	9.8	5.63	1.14	1.60	1.35	1.47	1.51
13	October	N[a]	29.3	4.97	0.86	1.62	1.31	1.51	1.47
14	"	N[b]	29.3	4.86	0.88	1.73	1.35	1.47	1.34
15	"	N[c]	29.3	4.19	0.80	1.37	1.07	1.12	1.19
16	"	N[d]	29.3	5.10	0.94	1.49	1.31	1.55	1.45
Check		None	....	5.37	0.89	1.26	1.23	1.36	1.27

[a] Ammonium nitrate.
[b] Ammonium sulfate.
[c] Urea.
[d] Ureaform.

Table 16. — Percent annual trunk diameter growth increase of treated trees over that of untreated trees in the pin oak time-of-application fertilizer plot in the Morton Arboretum. Trees were fertilized in 1964, 1965, and 1966.

	Percent Growth Increase Over Untreated Trees							
	Season of Application				Nitrogen Source			
Year	April	April June	April June October	October	Ammonium Nitrate	Ammonium Sulfate	Urea	Ureaform
1964	57	28	30	—2	26	46	29	12
1965	53	43	43	23	42	57	39	25
1966	15	19	11	2	15	19	5	9
1967	8	1	9	4	2	13	—2	8
1968	11	—1	10	7	6	8	0	14

Table 17. — Trunk diameter growth of white ashes in 1964 and 1965 in the rate-of-application fertilizer plot at the Morton Arboretum. Five trees per treatment were fertilized in 1964 and 1965.

	Trunk Diameter Growth, cm					*Percent Increase Over Untreated*
Rate of N, g/sq m	Ammonium Nitrate	Ammonium Sulfate	Urea	Ureaform	*Av.*	
14.7	2.37	1.83	1.83	1.67	*1.93*	15
29.3	3.28	2.32	2.13	2.02	*2.44*	45
44.0	2.24	2.41	2.35	2.88	*2.47*	47
58.6	2.46	2.84	2.88	2.30	*2.62*	56

cussed tests, clearly indicate that as more nitrogen is applied to the soil more growth will result. At 14.7 g per sq m, growth was increased 15 percent; at 29.3 g, growth was increased 45 percent; at 44.0 g, growth was increased 47 percent; and at 58.6 g, growth was increased 56 percent above that of untreated controls. These treatments caused no injury to turf or trees.

RESPONSE TO SOURCE OF NITROGEN. —Data used in comparing the source materials for nitrogen were obtained in the tests on *method of application* (Tables 11, 12, 13, 14), *time of application* (Tables 15, 16), and *rate of application* (Table 17). There was little difference in growth response to the four nitrogen source materials used. On oaks, ammonium nitrate was slightly more effective than urea, and ammonium sulfate was slightly more effective than ammonium nitrate. On ash trees, ammonium nitrate, ammonium sulfate, urea, and ureaform gave approximately equal responses. On locusts, ammonium nitrate was slightly more effective than urea. Ureaform releases nitrogen more slowly than the other three materials and tended to produce less growth in the first year of treatment and slightly greater growth in succeeding years.

SPECIES RESPONSE TESTS.—Data on the response of seven species of trees in the Morton Arboretum to nitrogen fertilization came primarily from 30-year-old, crowded, and slow-growing trees. The determinations of annual growth of these trees are given in Table 18.

The increased growth due to fertilization was greatest on swamp white oak, red maple, and red oak (Table 18). The swamp white oaks were the smallest trees of the seven species, were the slowest growing when untreated, and gave the greatest increase in growth

Table 18. — Trunk diameter growth of trees in the species response fertilizer plots at the Morton Arboretum. Trees were fertilized in 1964, 1965, and 1966.

Species	*Treatment*[a]	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*					*Percent Increase Over Untreated*
			1964	1965	1966	1967	*Total*[b]	
Basswood	N surface	24.3	0.41	0.58	0.51	0.56	*1.50*	15
	None	24.9	0.36	0.53	0.41	0.48	*1.30*	...
Norway maple	N surface	18.0	0.30	0.41	0.28	0.36	*0.99*	—19
	None	21.0	0.38	0.51	0.33	0.38	*1.22*	...
Red maple	N surface	18.6	0.33	0.48	0.25	0.30	*1.06*	61
	None	17.9	0.18	0.25	0.23	0.23	*0.66*	...
Sugar maple	N surface	17.2	0.25	0.30	0.20	0.30	*0.75*	—1
	None	17.0	0.20	0.33	0.23	0.28	*0.76*	...
Red oak	N surface	16.8	0.28	0.58	0.56	0.51	*1.42*	30
	None	14.2	0.25	0.41	0.43	0.43	*1.09*	...
Swamp white oak	N surface	12.2	0.41	0.51	0.51	0.56	*1.43*	170
	None	12.2	0.10	0.15	0.28	0.25	*0.53*	...
White oak	N surface	44.9	0.25	0.43	0.33	0.46	*1.01*	—17
	None	45.8	0.36	0.48	0.38	0.51	*1.22*	...

[a] Ammonium nitrate.
[b] 1964, 1965, and 1966 data only.

once fertilized. The trees in the fertilized basswood plot also grew more than trees in the unfertilized plot. The trees in the fertilized plots of sugar maple, Norway maple, and white oak grew less than those in the untreated plots.

Competition between the larger trees, sugar maple, Norway maple, and white oak, apparently limited the stimulatory effect that an added supply of plant nutrients often provides. The annual diameter increase of these three species of trees was approximately 0.4 cm. Younger, more widely spaced trees in the *method-of-application* test frequently increased in diameter by 1.2–1.6 cm per year. The plots of sugar maple, Norway maple, and white oak are the only plots of deciduous trees in this study that failed to show increased growth following soil application of nitrogen fertilizers.

Natural History Survey Arboretum

All species of trees at the Natural History Survey arboretum responded positively to fertilization. The average diameter growths of treated and untreated trees are given in Table 19.

Increased growth due to fertilization was 55 percent for hawthorns, 45 percent for lindens, 29 percent for Norway maples, 16 percent for Chinese elms, and 15 percent for green ashes. The trees that showed the slowest growth when untreated, hawthorn and linden, gave the greatest percentage increases in growth when treated. The substantial growth increase in 1965 over that in 1964 for all species except hawthorn was likely a result of favorable climatic conditions. The hawthorns were partially defoliated by the fungus *Entomosporium maculatum* Lev. during the summers of 1965 and 1966, which may have limited the response of this species to fertilization.

Sinnissippi Forest

The three species of deciduous trees at Sinnissippi Forest—green ash, sycamore, and black walnut—all benefited from the application of fertilizers. The amounts of annual diameter growth are given in Table 20. Walnut, the slowest growing species, responded with the greatest percentage growth increase following fertilization. Sycamore, the fastest growing species, responded with the lowest percentage growth increase. The average

Table 19.—Trunk diameter growth of trees in the species response fertilizer plots at the Natural History Survey arboretum. Trees were fertilized in 1964, 1965, and 1966.

Species	*Treatment*[a]	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*				*Percent Increase Over Untreated*
			1964	1965	1966	*Total*	
Green ash	N surface	2.4	0.97	1.93	1.50	*4.40*	15
	None	2.8	0.86	1.50	1.45	*3.81*	. . .
Chinese elm	N surface	1.9	1.73	2.29	1.73	*5.75*	16
	None	2.4	1.47	1.88	1.60	*4.95*	. . .
Hawthorn	N surface	2.4	0.74	0.66	0.64	*2.04*	55
	None	2.1	0.36	0.48	0.48	*1.32*	. . .
Littleleaf linden	N surface	1.2	0.28	0.86	1.17	*2.31*	45
	None	1.3	0.25	0.53	0.81	*1.59*	. . .
Norway maple	N surface	1.7	0.84	1.45	0.84	*3.13*	29
	None	1.7	0.64	1.07	0.71	*2.42*	. . .

[a] Ammonium nitrate.

Table 20.—Trunk diameter growth of trees in the method-of-treatment fertilizer plots at Sinnissippi Forest. Trees were fertilized in 1965, 1966, and 1967.

Species	*Treatment*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*					*Percent Increase Over Untreated*
			1965	1966	1967	1968	*Total*[a]	
Green ash	N surface	10.5	0.50	0.51	0.77	0.51	*1.78*	65
	PK surface	11.6	0.36	0.29	0.54	0.40	*1.19*	10
	NPK surface	11.4	0.56	0.57	0.90	0.75	*2.03*	88
	NPK holes	11.4	0.43	0.58	0.87	0.63	*1.88*	74
	None	11.3	0.25	0.32	0.51	0.47	*1.08*	. . .
Red pine	N surface	13.7	0.25	0.08	0.19	0.13	*0.52*	—20
	NPK surface	13.8	0.25	0.09	0.15	0.13	*0.49*	—25
	NPK holes	15.0	0.28	0.16	0.24	0.26	*0.68*	5
	None	13.8	0.24	0.17	0.24	0.32	*0.65*	. . .
Sycamore	N surface	12.1	0.58	0.39	0.50	0.41	*1.47*	11
	NPK surface	10.5	0.75	0.49	0.83	0.50	*2.07*	57
	NPK holes	13.0	0.40	0.45	0.74	0.40	*1.59*	20
	None	13.0	0.35	0.36	0.61	0.36	*1.32*	. . .
Black walnut	N surface	10.3	0.71	0.53	0.74	0.55	*1.98*	254
	NPK surface	10.4	0.52	0.40	0.55	0.20	*1.47*	163
	NPK holes	10.9	0.51	0.50	0.64	0.49	*1.65*	195
	None	10.8	0.17	0.15	0.24	0.13	*0.56*	. . .

[a] 1965, 1966, and 1967 data only.

annual diameter growth after fertilization of each of the deciduous species was approximately 0.6 cm.

The large, closely spaced pines at Sinnissippi Forest did not increase markedly in trunk diameter following fertilization. The fertilized pines in one plot grew more than the untreated trees, while the fertilized pines in two plots grew less than the untreated trees.

Even on the sandy soil at this site, nitrogen was the single nutrient that produced a significant growth response. Ash and sycamore trees receiving NPK grew more than those receiving N alone. Walnut trees receiving NPK grew less than those receiving N alone. Increased growth due to fertilizers containing nitrogen was 204 percent for walnut, 76 percent for ash, and 29 percent for sycamore.

There was little difference in growth

response between surface and soil hole methods of application. There was a tendency for fertilizers applied in holes to give slightly less response than surface-applied fertilizers during the first year of treatment and to give slightly more response as a residual action in the year following application.

Lincoln Trail State Park

Fertilized trees in every plot at Lincoln Trail State Park grew more than the untreated trees. Loblolly pines and tulip trees grew moderately well without fertilizers during the period of this test but the persimmon, sweet gum, and sycamore trees grew slowly. The amounts of growth of treated and untreated trees are given in Table 21.

The four deciduous species responded with greater percentage increases in growth than did the loblolly pines. The treated persimmons and sycamores grew about three times as fast as untreated trees. The increased growth of treated over untreated trees was about 60 percent for tulip trees, about 40 percent for sweet gums, and about 30 percent for loblolly pines.

The trees fertilized with NPK did not consistently grow more than the trees receiving only N. Among the sweet gums and tulip trees, one plot of trees receiving NPK grew more than, while another grew less than, trees receiving N alone. Persimmons receiving NPK grew more than those receiving only N. Sycamores receiving NPK grew less than those receiving N alone.

One method of application at Lincoln Trail State Park was not consistently better than another. The sweet gums and tulip trees receiving NPK on the surface grew more than comparable trees fertilized with NPK in holes, while the reverse was true with sycamores. There was a tendency for the trees treated with NPK on the surface to respond more than trees treated either with NPK in soil holes or N on the surface.

Crab Orchard Wildlife Refuge

The three species of trees at Crab Orchard Wildlife Refuge—sweet gum, pecan, and black walnut—all responded favorably to fertilization. The amounts of growth of the treated and untreated trees are given in Table 22. Particularly

Table 21.—Trunk diameter growth of trees in the method-of-treatment fertilizer plots at Lincoln Trail State Park. Trees were fertilized in 1966, 1967, and 1968.

Species	*Treatment*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*				*Percent Increase Over Untreated*
			1966	1967	1968	*Total*	
Loblolly pine	N surface	14.4	0.64	1.42	0.65	*2.71*	32
	NPK surface	14.3	0.68	1.53	0.56	*2.77*	34
	None	12.4	0.54	1.07	0.45	*2.06*	...
Persimmon	N surface	9.3	0.35	0.50	0.56	*1.41*	143
	NPK surface	9.2	0.44	0.63	0.72	*1.79*	209
	None	9.3	0.22	0.19	0.17	*0.58*	...
Sweet gum	N surface	11.7	0.44	0.78	0.85	*2.07*	41
	NPK surface	10.8	0.42	0.85	1.03	*2.30*	56
	NPK holes	10.8	0.42	0.60	0.73	*1.75*	19
	None	10.2	0.37	0.51	0.59	*1.47*	...
Sycamore	N surface	8.1	0.80	1.37	0.96	*3.13*	273
	NPK surface	7.6	0.54	0.96	0.83	*2.33*	177
	NPK holes	7.6	0.62	1.04	1.01	*2.67*	218
	None	9.5	0.32	0.33	0.19	*0.84*	...
Tulip tree	N surface	10.6	0.70	1.03	1.48	*3.21*	48
	NPK surface	10.1	0.75	1.23	1.92	*3.90*	80
	NPK holes	10.5	0.72	1.00	1.44	*3.16*	46
	None	11.4	0.60	0.68	0.89	*2.17*	...

Table 22. — Trunk diameter growth of trees in the species response fertilizer plots at Crab Orchard National Wildlife Refuge. Trees were fertilized in 1966, 1967, and 1968.

Species	*Treatment*	*Average Initial Diameter, cm*	*Trunk Diameter Growth, cm*				*Percent Increase Over Untreated*
			1966	1967	1968	*Total*	
Sweet gum	N surface	9.5	0.20	0.36	0.39	*0.95*	16
	NPK surface	10.3	0.28	0.46	0.48	*1.22*	49
	NPK holes[a]	8.6	0.18	0.41	0.44	*1.03*	26
	None	10.2	0.23	0.26	0.33	*0.82*	...
Pecan	N surface	40.1	0.89	0.85	1.06	*2.80*	16
	NPK surface	39.1	0.89	0.92	1.03	*2.84*	19
	None	42.5	0.81	0.68	0.93	*2.42*	...
Walnut[b]	N surface	19.1		0.76	0.36	*1.12*	53
	NPK surface	15.2		0.69	0.33	*1.02*	40
	None	17.7		0.48	0.25	*0.73*	...

[a] N on surface in 1967 and 1968.
[b] Trees were fertilized in 1967 and 1968 only.

satisfying was the demonstrated diameter growth increase of at least 16 percent by the large, widely spaced pecan trees. Sweet gums increased their growth by more than 30 percent, and the walnuts increased theirs by more than 40 percent, following fertilization. Nitrogen was the nutrient that produced the significant growth response in all species; however, two plots of sweet gum receiving NPK grew somewhat more than one plot receiving N alone.

DISCUSSION AND CONCLUSIONS

Although there is certainly a need for more field trials to evaluate the effects of fertilizers on established deciduous trees, the requirements for carefully controlled experiments of this nature are exceedingly demanding. Uniformity of site, soil, and specimen material is essential. The ideal plant material should be from clonal stock. If seedling stock must be used, it should come from the same source and be collected, planted, and transplanted as a unit. It often requires 3 years for a seedling 1–1.5 m tall to become well established following transplanting. Growth during these years is limited.

A restricted soil area frequently limits tree growth because of competition among plants for available water, nutrients, or light. Visual observations of tree crowns are usually adequate for determining competition for light. Root distribution, however, varies with plant species and soil type and cannot be accurately estimated. Thus trees must be widely spaced, and not in competition with other trees, if meaningful measurements of increased growth due to the addition of nutrients are to be made. An experimental area containing established, uniform trees that are widely spaced on a uniform soil is rare.

Several factors have previously been used to measure the responses of trees to fertilizers, one of which is leaf color. The leaves on many trees become more green or darker green following the application of nutrients. Color data presented in an earlier report (Himelick, Neely, & Crowley 1965) were collected in 1963 and 1964 from plots at the Morton Arboretum. These data correlated well with the data from trunk diameter growth measurements.

Tree height, shoot growth, and trunk diameter growth can all be used to measure growth responses to fertilization. Each has advantages and disadvantages. Trunk growth extends throughout the growing season and the amount of this growth is influenced by the amount of soil moisture available. Trees must have an established root system before trunk diameter measurements will indicate growth stimulation due to fertilization. Shoot growth of many trees occurs during a relatively short period early in the growing season with possible recurrent flushes of growth later in the season. In other trees, however, shoot growth may occur over a longer period of time. Shoot growth has not been as well correlated with climatic factors as has trunk growth. The obvious difficulty of accurately determining the height of large trees, and the large number of measurements required for adequately sampling shoots on large trees, prohibited the use of these means of measuring tree growth in this study.

The results of this study on the responses of established trees to fertilizers do not indicate the need for radical changes from current practices in fertilizing trees. However, the results do give a good means of comparing time, rate, and method of fertilizer applications, and the nutrients that may stimulate growth response.

In our tests at five sites in Illinois, significant growth response was obtained only from nitrogen. This is not surprising, because nitrogen is the element that most frequently stimulates the growth of other plants. Moreover, an optimum supply of nitrogen is often lacking in most soils of inorganic origin.

The soils at the five test sites represented sandy soils, fertile deep topsoils of prairie origin, fertile shallow topsoils of forest origin, and infertile shallow topsoils with heavy clay subsoils. Regardless of soil type, nitrogen stimulated growth in deciduous trees. Other nutrients, although they were available in relatively low quantities in some of the soils, failed to stimulate growth when added as fertilizers.

The four sources of nitrogen used in these tests were equally beneficial. Ammonium nitrate, ammonium sulfate, and urea release nitrogen rapidly in the soil, making it readily available for plant use. Ureaform releases nitrogen more slowly. It is less effective in the first year of application but has a greater residual influence than the other nitrogen sources tested.

Soil surface, soil hole, and solution injection were almost equally effective methods of applying nitrogen fertilizers. There is a great difference, however, in the economic aspects of application by these three methods. Solution injection is slow and expensive because it requires soluble fertilizers and a hydraulic system for injection. Placing dry fertilizer in soil holes is slow, difficult, and expensive because it requires extensive time and manpower to prepare the soil holes and distribute the fertilizer. Broadcasting on the surface is fast, easy, and relatively inexpensive. It requires only a lawn fertilizer spreader and a nitrogen fertilizer.

In this study the growth response to foliar fertilization was extremely slight. The color response given in the preliminary report (Himelick, Neely, & Crowley 1965) was just as slight. Soil applications of fertilizers gave significant growth and color responses, while foliar applications did not.

The rate of application of nutrients used in these tests was an empirical figure. It was based on area of soil, not size of trees. Nitrogen at the rate of 29.3 g per sq m (6 lb per 1,000 sq ft) of soil area is commonly used for fertilizing established shade trees. Arborists placing dry fertilizers in holes use this rate commercially, and have found it nontoxic to trees and grass. Our results confirm the usefulness of the rate. The trees fertilized with one-half this rate grew less than half as much as the trees fertilized at this rate. The trees fertilized with additional nitrogen grew more, but the additional growth was insufficient to justify changing the recommendations. Higher rates of nitrogen applied to the surface during summer months were toxic to grass (Himelick, Neely, & Crowley 1965).

Spring applications of nitrogen were

more effective than summer and fall applications. The distinct advantage of April over October applications obtained in this study is not in agreement with the research of Jacobs (1929) or Chadwick (1941).

There is little in the results of this study on which to base recommendations on frequency of fertilization. In most of our tests, the trees were fertilized for 3 consecutive years. The amount of additional growth due to fertilization was relatively uniform each year with little or no cumulative effect. Within 2 years after fertilization ceased, the treated trees were growing at the same rate as the untreated trees.

Although 20 species of deciduous trees were included in this study, it is difficult to reach conclusions concerning the inherent capabilities or genetic limitations of tree species in response to fertilization. At four of the five sites the slow-growing tree species gave the greatest percentage increases in growth when fertilized, but they did not necessarily produce a greater volume of wood than the faster-growing trees. The slow-growing trees were the smaller trees at these sites. Tree size and tree competition rather than tree species more likely influenced the degree of response to fertilization.

At no time during the 6 years of this study was there injury to grass or understory plant material following surface application of N or NPK fertilizers. The fertilized understory plants became darker green and grew larger than comparable unfertilized plants. Fertilized trees grew more than unfertilized trees even with the additional competition from weeds and bluegrass turf.

In Illinois there usually is an adequate supply of rainfall during the months of April, May, and June. During the period of these tests, rainfall in April, May, and June usually amounted to 25–35 cm (10–14 inches) at each of the five tree fertilization test sites (Table 2). Periods of drought are more common during the other 9 months of the year. During one 3-month period rainfall totals may be two or three times greater in one year than in the same period of the previous year.

Annual variations in tree growth are partly determined by the amount of soil moisture present. Due to variability in frequency and intensity of rainfall and variability in soil characteristics, it is very difficult to determine soil moisture content from rainfall data. In an attempt to associate amounts of rainfall with tree growth, two correlations were found. There was little divergence of pin oak, white ash, and honey locust trees in the *method* test at Morton Arboretum from the pattern of little growth in 1963, increased growth in 1964, increased growth in 1965, decreased growth in 1966, increased growth in 1967, and decreased growth in 1968. Both the amount of rainfall from October through March, prior to the growing season, and the amount from June through August, during the growing season, were correlated with the trunk diameter growth of trees (Fig. 8). These correlations were found to exist on many species of trees at all five sites in this study.

Recommendations for shade tree fertilization to arborists and homeowners were prepared by Neely & Himelick (1966). The recommendations were based primarily on this study with additional information gleaned wherever possible from experiments in aboriculture, pomology, forestry, and agronomy.

SUMMARY

The responses of established trees to applications of fertilizers at five sites in Illinois were determined by annual trunk circumference measurements. As many as 16 treatments (each of the treatments a different combination of fertilizer and method or time or rate of application) were used on 20 species of deciduous trees and 2 species of evergreens. Four methods of application were used: surface broadcasting, placement of dry

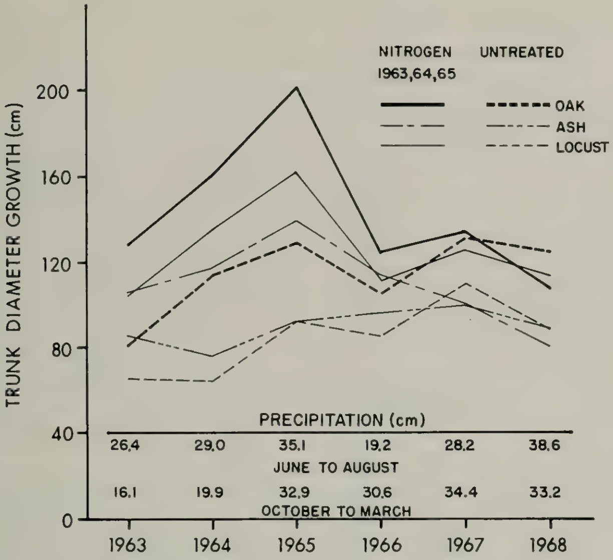

Fig. 8. — The diameter growth of three species of trees in the method test at Lisle was correlated with the quantity of precipitation occurring in (i) 6 fall and winter months prior to the growing season and (ii) 3 summer months during the growing season.

fertilizers in holes in the soil, injection of liquid fertilizers into the soil, and spraying of foliage. The following nutrient elements or combinations of elements were used: N, PK, NPK, and NPK plus minor elements.

When elemental nitrogen was added to the soil at the rate of 29.3 g per sq m (6 lb per 1,000 sq ft), tree growth increased significantly. Increased growth persisted only 1 or 2 years after treatment ceased. April applications increased growth more than October applications.

The application of phosphorus and potassium to the soil did not bring about a significant growth response; nor did a combination of phosphorus, potassium, and nitrogen produce a response that was significantly greater than that produced by nitrogen alone. The addition of minor elements to NPK produced no significant growth response.

The three methods of soil application appeared to be about equally effective, with minor variations among the tree species. Foliar sprays did not produce a substantially greater growth than the growth of unfertilized trees.

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A Survey of the Mussels (Unionacea) of the Illinois River: a Polluted Stream

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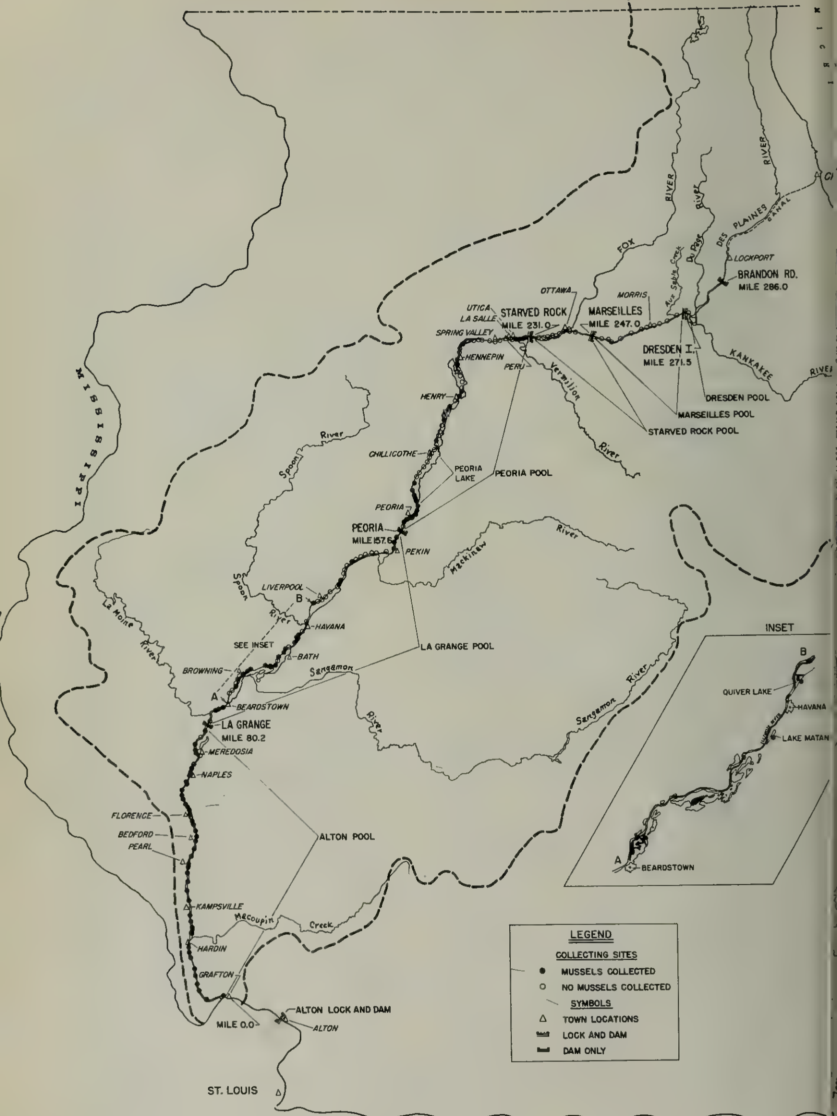

Fig. 1.—Sites on the Illinois River where attempts were made to collect live mussels in the 1966 sur
966 subfossil mussel collecting sites are not shown.

A Survey of the Mussels (Unionacea) of the Illinois River: a Polluted Stream

William C. Starrett

EARLY IN THIS CENTURY Danglade (1914:8) considered the Illinois River the most productive mussel stream per mile in this country. At that time mussel shells were in great demand for use in manufacturing buttons. About 1910 more than 2,600 boats were engaged in mussel fishing on the Illinois River between Peru and Grafton, Illinois (Ibid.) (Fig. 1). The maximum commercial shell yield from the Illinois River occurred in 1909 and amounted to thousands of tons of good button shells (Ibid.). Very few statistics are available specifically for the Illinois River; however, to give some indication of the magnitude of the harvest, one shell buyer informed Danglade (1914:16) that in 1911 he bought 600 tons of shells from just two landings in the vicinity of Peoria, Illinois.

Before 1907 most of the mussel fishing on the Illinois River was done by pearl hunters (Danglade 1914:8 & 31).[1] One pearl found in a mussel taken in 1911 from the Illinois River at Chillicothe was valued at $3,000 (Danglade 1914:15). After 1906 mussels were taken from the Illinois River primarily for the sale of shells to button-shell buyers, and the pearls and slugs were of secondary consideration.

By 1911 mussels in certain parts of the Illinois River were beginning to be affected by pollution, siltation, and mussel fishing (Forbes & Richardson 1913; Danglade 1914:48). The adverse effects of pollution on the fishes and wildlife of the Illinois River during the first half of this century have been discussed by Mills, Starrett, & Bellrose (1966). After World War II the great increase in the use of plastics in button manufacturing had a further serious effect on the few mussel fishermen remaining along the Illinois River.

About 1962 a renewed interest in mussel fishing on Illinois streams was stimulated by the market demand for Illinois shells by the Japanese pearl-culture industry. Earlier the Japanese had obtained most of their shells from the Tennessee River system, but due to the decline of this natural resource in those waters, the buyers had to look for new sources farther north.

Pearl culturists have found that a calcareous nucleus inserted into the oyster (*Pinctada*) is the best material to use for a pearl to form around (Cahn 1949:48). According to Cahn (1949:49):

> "As nuclei range in diameter to a maximum of more than six millimeters, the first requirement for their production is a heavy, solid shell. Most nuclei are prepared from the shells of fresh-water mollusks. Unfortunately for the industry, Japan produces no bi-valve with a shell thick enough to produce nuclei of the larger diameters in quantities sufficient to supply the demand. Search for the desired material led to the United States where admirable shell material finally was found in enormous quantities in the *Amblema, Quadrula, Pleurobema,* and *Megalonais* species from the Mississippi River and its major tributaries. All have massive shells and were found to yield a high proportion of satisfactory nuclei similar in hardness and specific gravity to the superimposed nacre."

---

[1] For further information on the pearl industry of the Illinois River and various parts of the world, see Vertrees' (1913) book *Pearls and Pearling.*

Lopinot (1967:15) mentioned that shells produced in Red China also are suitable for use as nuclei in pearl culture.

As a result of the new Japanese market for shells from Illinois waters, the sales of Illinois mussel fishing licenses rose from 69 in 1961 to 1,279 in 1966 (Lopinot 1967:12 and pers. comm., 18 January 1968). From the larger Illinois streams the best grade of shells for use in pearl culture occurs in the Wabash River, the next in the Illinois River, and the third in the Mississippi River. The 1966 commercial mussel (shells) catch from the Illinois River as reported by the exporters was 1,118.40 tons valued at $109,460.83; for the entire state of Illinois it was 3,557.65 tons valued at $604,307.83 (Lopinot, pers. comm., 5 June 1967).

Soon after the increase in mussel fishing in the early 1960's, Messrs. William J. Harth and Alvin C. Lopinot of the Illinois Department of Conservation and the author realized that no current information was available concerning the state's mussel fauna and the new mussel fishery. The laws at that time on mussel fishing in Illinois were designed to cope with the old fishery involved in selling shells to the button manufacturers rather than with the new Japanese market requiring large shells of a limited number of species. Studies of mussels were needed on the Wabash, Illinois, and Mississippi rivers. Indiana has since made studies of the mussels of the Wabash River, and these studies should be of benefit to Illinois (Bingham 1968; Meyer 1968). In 1966 Lopinot (1967) made a general study of the commercial aspects of the new mussel fisheries of the Wabash, Illinois, and Mississippi rivers. The author has been studying the biology and chemistry of the Illinois River and its bottomland lakes relative to pollution for a number of years. Since a considerable amount of old base-line data on the mussels of the Illinois River (Calkins 1874; Kelly 1899; Baker 1906; Forbes & Richardson 1913; Danglade 1914; and Richardson 1928) were available for comparisons with data on the present mussel fauna, the author was interested in expanding his studies to include an investigation of the mussels of that river. Additional funds were made available to him in 1966 and 1967 for such a study by the Bureau of Commercial Fisheries (U.S. Fish and Wildlife Service) and the Illinois Department of Conservation.

The basic purposes of this investigation were to make a survey of the pearly mussel (Mollusca: Pelecypoda: Unionacea) populations of the entire Illinois River in order to formulate a sound basis for managing the mussel resource of this river, and to determine what species and distributional changes had taken place during the past century.

The manuscript was reviewed by Dr. David H. Stansbery of The Ohio State Museum and The Ohio State University and was edited by Robert M. Zewadski of the Illinois Natural History Survey. The first draft of the section in this paper titled "Mussel Fauna of the Illinois River" was read by Dr. Joseph P. E. Morrison of the U.S. National Museum, Dr. Paul W. Parmalee of the Illinois State Museum, and Dr. Henry van der Schalie of the University of Michigan Museum of Zoology.

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THE ILLINOIS RIVER

The Illinois River is formed by the confluence of the Kankakee and Des Plaines rivers southwest of Chicago (Fig. 1). Since the completion of the Chicago Sanitary and Ship Canal in 1900 water has been diverted in varying amounts (maximum 10,000 cfs) from Lake Michigan at Chicago (including domestic and industrial water pumped from Lake Michigan and later dumped into the canal as treated and untreated wastes) through the canal to the Des Plaines River at Lockport and thence into the Illinois River. The Illinois River proper (Fig. 2) is 272.9 miles in length and the entire waterway from Lake Michigan to the mouth of the Illinois River at Grafton (Mississippi River) is 327 miles. The river and its tributaries have a drainage basin of 32,081 square miles (Barrows 1910:1). The maximum discharge of the Illinois River at Kingston Mines (river mile 145.3) in the water year 1965-1966 was 51,700 cfs, the mean discharge was 16,188 cfs, and the minimum discharge was 3,990 cfs (United States Geological Survey 1967:132).

> "The Illinois Valley is naturally divided into an upper and a lower part. The upper Illinois, comprising the westward-flowing section from the junction of the Des Plaines and Kankakee to the great bend near Hennepin, is independent of preglacial drainage lines and is excavating a new course, its bed being usually on the rock. The lower Illinois, extending from the great bend to the mouth, occupies the preglacial channel, in which the rock bottom lies nearly 100 feet below the bed of the present stream.
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> "The old river channel of the lower Illinois is much too large for the present volume of flow, so that it has been filled up by alluvial deposits forming the present bottom lands. The deposition of material has also been aided by the flat slope of the stream, the fall in the lower 223 miles being only 33 feet" (Hoskins, Ruchhoft, & Williams 1927:4–5).

Formerly, between La Salle and Grafton there were about 400,000 acres of bottomlands subject to overflow by the Illinois River. Some of these overflow lands were in permanent bottomland lakes connected with the river. During the first part of the century nearly 200,000 acres of these bottomlands and lakes were drained and leveed off from the river for agricultural purposes. One of these, Thompson Lake, near Havana in Fulton County, was drained in the early 1920's. The mollusca of this former bottomland lake were studied before 1900 by Strode (1891*a* and 1891*b*).

Fig. 2.—The Illinois River below Pekin in the La Grange navigation pool at river mile 148.0. Photo by W. D. Zehr.

Presently about 8,000 acres of abandoned drainage districts have been restored as bottomland lakes (type 58) (Hutchinson 1957:123–125). In the current study, mussel collections were made in two of these lakes, Lake Matanzas and Meredosia Lake. The collecting site referred to as Quiver Lake, near Havana in Mason County, is merely a large slough connected with the river.

River Mile and Bank

The Illinois River is a navigable stream, and the boat channel is well marked with buoys, lights, and markers. These navigational aids are located in detail in the U.S. Army Engineer District, Corps of Engineers, Chicago, Illinois, publication *Charts of the Illinois Waterway from Mississippi River at Grafton, Illinois to Lake Michigan at Chicago and Calumet Harbors.* In this paper references are made to river miles based on the Corps of Engineers' chart book of the Illinois Waterway. A river mile designation is the exact number of miles upstream from the mouth of the river at Grafton.

The engineering designation of the sides of the river adjacent to the channel is used here and is termed "bank." The bank side is the left bank (LB) or right bank (RB) as viewed from midstream by the observer facing downstream.

Dams and Navigation Pools

> "Before 1900, low dams were built at Marseilles, Henry, Copperas Creek, La Grange, and Kampsville. Because they were low, their greatest effect on the stream was during periods of low water" (Mills, Starrett, & Bellrose 1966:5).

In the 1930's higher dams with locks for navigation were constructed on the Illinois River to help maintain a 9-foot channel. These locks and dams were built at Dresden Island (24 feet at river mile 271.5), Marseilles (24 feet at river mile 247.0), Starved Rock (19 feet at river mile 231.0), Peoria (11 feet at river mile 157.6), and La Grange (10 feet at river mile 80.2). The lower part of the river is under the influence of the Alton dam on the Mississippi River (Fig. 1). The waters impounded by these dams are called navigation pools, and throughout this paper references are made to these pools as the geographic locations of the various sections of the river. The lower section of the river is the Alton pool (river miles 0.0–80.2); the La Grange pool is between the La Grange dam and the Peoria dam (river miles 80.2–157.6); the Peoria pool is between the Peoria dam and the Starved Rock dam (river miles 157.6–231.0); the Starved Rock pool is between the Starved Rock dam and the Marseilles dam (river miles 231.0–247.0); the Marseilles pool is between the Marseilles dam and the Dresden Island dam (river miles 247.0–271.5); and the Dresden pool of the Illinois River covers only the lower 1.4 miles of this pool impounded by the Dresden Island dam (river miles 271.5–272.4); the remaining upper part of this pool is the Des Plaines River.

Current Speed

> "The fall in the Illinois River is but slight—an average of .267 of a foot per mile of its total length. Fifty and seven tenths feet of this fall occur in the first forty-two miles of its course, and from Utica to the mouth of the river the total fall is but 31 feet, or an average of .137 of a foot to the mile. The effect of this slight fall is seen in the sluggish current of the Illinois, which ranges from .4 of a mile per hour at the lowest water to 1.737 miles when at twelve feet above low-water mark. The usual rate of flow for ordinary stages varies, however, from 1¼ to 2½ miles per hour" (Forbes & Richardson 1920:xl–xli).

These records of current speeds were made before 1908. Observations made in the present study reveal that the river is now more sluggish than it was in the early part of this century. At ordinary river stages the current speed now is only about 0.6 mile per hour. The increase in sluggishness of the river is believed by the author to be a result of the higher dams now on the river and the reduction in diversion of water from Lake Michigan.

In the Alton and La Grange pools (1966) the current ranged from 0.5 to 1.1 miles per hour. During low river stages the current is sometimes not perceptible in the midpart of the La Grange pool (river mile 113.1). In the extreme lower part of the Peoria pool the river is rather narrow (river miles 157.6–162.8) and the current here in 1966 ranged from 0.4 to 1.1 miles per hour. Between river miles 162.8 and 179.2 the river is 1–2 miles in width and is referred to as Peoria Lake (Lower, Middle, and Upper Peoria lakes). No current was perceptible in Peoria Lake except at the narrow part of the river connecting Lower and Middle Peoria lakes ("Narrows" at river mile 166.7) where the current was 0.9 mile per hour. In the remainder of the Peoria pool (river miles 179.2–231.0) the river is typical of much of the stream, and the current here ranged from 0.2 to 0.6 mile per hour. Single current determinations were made in 1964 by the author in Starved Rock pool (0.6 mile per hour) and in the Marseilles pool (0.8 mile per hour).

Bottom Soils and Turbidity

Because of the heavy towboat traffic and dredging in the navigation channel, mussel fishing is largely confined to the waters adjacent to the channel. Therefore, we are particularly concerned with the bottom substrates lying between the navigation channel and the shoreline.

> "Soil pollution has been present in Illinois River waters since the recession of the last ice sheet. However, the laying bare of the soil in agricultural operations has greatly increased the problem" (Mills, Starrett, & Bellrose 1966:5).

In Illinois the sedimentation problem resulting from farming operations increased tremendously in the middle 1930's, as revealed by studies made by Brown, Stall, & De Turk (1947) and the author's personal observations on the Illinois River. This problem came about through the increase in the planting of row crops, particularly soybeans, and the advent of heavy, powered farm equipment. According to the Illinois Cooperative Crop Reporting Service (1965: 58–59), counties in Illinois partly or wholly drained by the Illinois River in 1964 had 6,220,200 acres planted to corn and 3,466,100 acres in soybeans. In other words, in 1964 about 47 percent of the watershed of the Illinois River in Illinois was in row crops. In 1966, 62 percent of private cropland in this country needed conservation treatment (Stall 1966:80).

The increase in the sluggishness of the river, as mentioned above, and the increased planting of row crops on the watershed have, in the author's opinion, made siltation in the past 30 years an important factor adversely affecting the survival of mussels and other organisms in the Illinois River and its bottomland lakes (river miles 0.0–231.0). A study made in 1950 on Lake Chautauqua, an Illinois River bottomland lake near Havana, revealed that sediment deposits had reduced the storage capacity of the lake by 18.3 percent in 23.8 years (Stall & Melsted 1951:1).

> "The sediments in Lake Chautauqua are mostly of a fine texture and form a loose, flocculent 'false bottom' (not similar to the type found in bog lakes) over the original lake bottom. A slight disturbance of the 'false bottom' causes particles to become resuspended and so increases the turbidity of the water" (Jackson & Starrett 1959:160).

The bottom of the river in the Alton, La Grange, and Peoria pools was chiefly hard mud overlaid in numerous areas with fine sediment deposits (soft-mud bottom) similar to the "false bottom" found in Lake Chautauqua. In some sections of the upper La Grange and Peoria pools the silt contained a mixture of fine sand particles. Very few clean sand or gravel bottoms were observed in the lower three navigation pools. As mentioned earlier, the bottom in the upper two pools (Starved Rock and Marseilles) was primarily rock. In some parts of these two pools the rock was overlaid with mud, sand, and/or gravel.

Turbidity readings (midchannel) made during minimum flow periods by the author are summarized in Table 1. The high turbidities observed in the lower two pools tended to reflect the silted conditions (soft-mud bottom) of the lower river and heavy silt loads brought into this section of the river by the tributary streams. On June 24, 1964, following a flash flood, the Illinois Sanitary Water Board determined the turbidity in one part of the Alton pool to be 2,000 turbidity units.

The author has made numerous observations on the effect a towboat has on turbidity in the various parts of the river. A towboat underway causes a strong current and washing action on the silt bottom ("false bottom") inshore, which resuspends the silt particles, thereby increasing the turbidity. The increase in turbidity is more noticeable in the lower three pools, particularly in the Alton pool, than it is upstream because of differences in bottom types as discussed above. The outrush of the water from shore toward the channel caused by a towboat also temporarily exposes the shallow areas. On November 18, 1964, in the Alton pool at river mile 65.1, the turbidity just prior to the passing of two towboats was 108 units, and within 6 minutes after the tows had passed, the turbidity was 320 units. Sixteen minutes later the turbidity had dropped to 240 units.

Table 1.—Ranges of turbidity (Jackson turbidimeter) during minimum flow periods in the navigation pools of the Illinois River (1963 through 1966)

Navigation Pool	*Range in Jackson Turbidity Units*
Alton	36–320
La Grange	60–220
Peoria	15–140
Starved Rock	15–52
Marseilles	15–47
Dresden	15–27

Pollution and Water Chemistry

The Illinois River has a long known record of pollution. The pollution of the river has been associated with the growth and expansion on its watershed of human populations, industries, and agriculture. The Illinois River Valley is sometimes referred to as the "Ruhr Valley" of the Midwest because of the tremendous number of industries located along the river.

> "Little concern was shown about changes in, or the changing of, the Illinois River for the first 250 years of its use by white people. Its character seemed to remain about the same, although the greatest flood ever recorded for the river was in the 1840's. Steamboats made their way far up its reaches in the 19th century. Cities sprang up along its shores and, near the headwaters, Chicago began its growth. Events happened rapidly from the last quarter of the 19th century to the present time.
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> "To give a simple illustration of the development in the river's basin, the population of the counties which are all or in part drained by the Illinois River changed from about a half-million in 1850 to 1,629,738 in 1870. By 1964 this figure had risen to 8,537,900 of a total state population of 10,500,000.
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> "The basic reason for the 1900 diversion of Lake Michigan water into the Illinois waterway was to dilute sewage and transport it away from Chicago. Since that time the treatment of sewage in the Chicago area has been greatly improved, but the rich effluent still affects the waters of the waterway below the city (Keup, Ingram, Geckler, &

> Horning 1965). Moreover, the other cities within the Illinois River basin have grown, and make their increasing demands on and contributions to the stream" (Mills, Starrett, & Bellrose 1966:4–5).

By 1911 the upper section of the Illinois River (Marseilles and Starved Rock pools and the upper section of the Peoria pool) was heavily polluted by untreated domestic and industrial wastes from the Chicago area (Forbes & Richardson 1913). During and immediately following World War I, pollution became even more severe and critically affected the river downstream as far as Peoria (Purdy 1930:10; Richardson 1928).

In the past 40 years conditions in the upper section of the river (Marseilles and Starved Rock pools) and Peoria Lake have improved as the result of the treatment of wastes, reduction of flow, and augmentation of pollution laws. In 1922 the population equivalent of domestic and industrial wastes emptied into the river was 6,211,471 (Hoskins, Ruchhoft, & Williams 1927:25), but by 1960 it had dropped to an equivalent of 2,417,000 people (United States Public Health Service 1963:III-1). However, the beneficial gains in pollution abatement during the past 40 years, reflected by the reduction in BOD (Biochemical Oxygen Demand, Table A-1[1]), that have occurred in spite of increases in human populations and industry on the watershed tend to be offset to a serious degree by the high concentration of ammonia nitrogen originating from treated and untreated effluents and possibly from agricultural fertilizers. In 1967 maximum determinations of ammonia nitrogen (N) ranged from 0.9 ppm in the lower river to 8.2 ppm in the upper Illinois River (Allan Poole, pers. comm., 11 March 1968). At river mile 274.0 in the Des Plaines River in 1967 the maximum determination of ammonia nitrogen was 26.0 ppm (Ibid.).

Dissolved oxygen now is considerably higher in the upper river and Peoria Lake than it was in the 1911-1928 period (Mills, Starrett, & Bellrose 1966:9). However, during the past 50 years the dissolved oxygen content of the river below the Peoria-Pekin metropolitan area has decreased. Also the dissolved oxygen content in part of the Peoria pool above Middle Peoria Lake is still critical. The midsummer dissolved oxygen determinations made by the author (Table A-2) and the chemical, radiological, and bacteriological determinations of the Illinois Sanitary Water Board (1967) presented in Table A-1 reflect the pollutional conditions of the river in 1966. The bacterial counts indicate pollution in the entire river in 1966.

The dissolved oxygen was usually relatively high in the upper parts of the navigation pools below the dams, and in midsummer it decreased downstream within the pools (Table A-2). In several of the pools, especially the Alton pool, where the reoxygenated water is subjected to very few additional domestic and industrial wastes, the dissolved oxygen would be expected to remain relatively high rather than to decline as shown in Table A-2. The continual decline in dissolved oxygen in these pools accompanied with a decrease in BOD is probably related to nitrification oxidation, as was demonstrated by the United States Public Health Service (1963:IX-21) in July of 1962.

In the early 1960's the United States Public Health Service (1963:V-26) determined these amounts of toxic metals in the Illinois River: (i) copper was less than 0.30 ppm; (ii) nickel ranged from 0.01 ppm to 0.25 ppm; (iii) zinc was as high as 0.13 ppm; and (iv) chromium varied from 0.01 ppm to 0.08 ppm.

Relative to detergents, Sullivan & Evans (1968:198–199) reported that in the Illinois River at Peoria (1.4 miles upstream from the outfall of the Greater Peoria Sanitary District treatment plant) the mean MBAS (methylene blue active substance) dropped from 15.7 tons per day in the 1959-1960 period to 9.0 tons per day in the 1965-1966 period as a result of the conversion from ABS detergents to the more readily biodegradable

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[1] The letter *A* designates that a table is in the Appendix of this paper.

LAS compounds. The author's 1966 ABS determinations from the Illinois River were about one-half of the amounts of his earlier determinations (Table A-2).

According to Verduin (1967:167–168):

> "The three important sources of phosphorus contribution to our waters are organic matter in sewage, phosphorus-containing detergents, and phosphorus in the runoff and drainage from farmlands, most of which receive heavy applications of phosphate fertilizers."

Mr. Allan Poole (pers. comm., 11 March 1968) informed the author that in 1967 total phosphates (PO_4) were as high as 8.3 ppm in the Marseilles pool and 5.7 ppm at Peoria. Sullivan & Hullinger (1969:216) in 1967 determined the mean total phosphorus concentration in Upper and Middle Peoria lakes to be 1.13 ppm, of which orthophosphates represented 75 percent of the total phosphorus; 64 percent of the total phosphorus was in a dissolved state. These authors (1969:215) mentioned that concentrations of total phosphorus in Peoria Lake were 17 to 94 times higher than those found in other bodies of water, according to the literature they reviewed. In the author's opinion treated sewage and industrial effluents (including detergents) were the main sources of phosphorus in the Illinois River. Even though the Illinois River was extremely rich in nutrients, algal blooms in the mainstream were limited by high turbidities and possibly by synergistic effects of toxic metals. When making dissolved oxygen and pH determinations on sunny days, the author found that primary production was quite limited in the mainstream of some parts of the river.

Biological data collected from the Illinois River by the author and his associates have revealed pollutional aspects not disclosed by chemical and bacteriological data (Mills, Starrett, & Bellrose 1966). These pollutional aspects with their effects on the mussels are discussed later in this paper.

Fishes

Mention of the fishes of the Illinois River is included here because of the fishes' role as hosts for the parasitic, or glochidium, stage of freshwater mussels.

Fig. 3.—An Illinois Natural History Survey crew electrofishing in the La Grange navigation pool of the Illinois River. Photo by Dr. George W. Bennett.

Certain species of mussels require a specific host fish for a short period of time, whereas other species are evidently able to use several kinds of fishes as hosts (Baker 1928:13). Many changes have occurred in the fish fauna of the river since 1907 and will be discussed in detail in a later paper by Starrett & Smith. Since 1950 the author has been studying the fishes of the Illinois River and its bottomland lakes (Starrett & Fritz 1965). In this period 101 species of fishes have been collected from the river and its bottomland lakes by the author (Fig. 3).

FIELD PROCEDURE

The mussel survey of the Illinois River was conducted from June 9 to October 28, 1966. Most of the collecting was done during the first 3 months of the program. A total of 429 collections was made for live mussels. The collections were made with an exploratory type of crowfoot bar (brail) and a mussel dredge and by wading (hand collecting) between river miles 0.9 and 272.0 (Table 2). In these collections 4,247 mussels were taken alive (Table A-3). An additional 20 live mussels were picked up by hand in the Aux Sable River near its mouth at Illinois River mile 268.2 in the Marseilles navigation pool. The shells of all of the live mussels collected in the survey were saved and taken back to the field laboratory of the Illinois Natural History Survey near Havana, Illinois, for identification and storage. (Several live mussels were obtained from commercial mussel fishermen operating in the Peoria pool in 1969, and the records of these shells are included in this paper.)

Upon the completion of a collection, the live mussels were placed in a gunny sack with a tag bearing the collection number. At the end of a day's collecting each collection of live mussels was weighed and steamed. The live mussels were weighed on a Chatillon scale to the nearest 0.01 pound. Each collection of mussels was placed in a steel canner for steaming; a portable two-burner Coleman stove was used in the field as the heat source. After the mussels of an individual collection were steamed, the shells were cleaned and a rubber band was tightly secured around each pair of valves. The cleaned shells of a collection were resacked for storage. The meats and the bottom of the canner were examined for pearls.[1]

A few live mussels from several parts of the river were cleaned with a knife and the fresh meats were wrapped in foil and frozen. Later these meats were checked by the electron capture gas chromatography method for the presence of organochlorine pesticides by Dr. W. N. Bruce of the Illinois Natural History Survey.

A 16-foot, square bow Arkansas Traveller boat powered by a 9½-horsepower outboard motor was used in making the crowfoot bar and mussel dredge collections of live mussels. The speed of the boat was adjusted to compensate for current speed variations in order to fish the mussel collecting devices at a uniform speed. A wooden stanchion was mounted near the bow of the boat and was used for securing the dredge boom and the crowfoot bar line.

A professional mussel fisherman was employed during the first 2 weeks of the program to serve in an advisory capacity to assure proper operation of the collecting devices.

The survey was designed to sample, on a stratified basis, as many different sites in the entire length of the river as was possible with one boat crew in a 3-month period (Table 2). The sampling sites included known former and existing mussel beds as well as other areas. Former mussel beds were located from reference points given in the literature (Danglade 1914; Forbes & Richardson 1913; and Richardson 1928), interviews with elderly commercial fishermen, and concentrations of old shells along the shoreline. Since 1964 the author had noted the areas where most of the commercial mussel fishing was being conducted. Those observations, coupled with interviews with active commercial musel fishermen, enabled us to locate the known productive mussel beds.

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[1] None of the few dozen small pearls and slugs found during the 1966 survey was of any commercial value.

The stratified basis of sampling was extended to the remainder of the river by attempting to select as collecting sites those habitats appearing to be the best for mussels. In conducting fish surveys with limited personnel and time on a large river like the Illinois, the author has found that the stratified, or selective, habitat sampling method gives

Table 2.—Illinois River locations by mile numbers[a] and bottomland lakes where mussel collecting was done in the 1966 survey.

Alton Pool		*La Grange Pool*		*Peoria Pool*		*Starved Rock Pool*	*Marseilles Pool*[d]
0.9	53.8	80.3	117.6	158.3	184.8	233.7	249.2
1.0	53.9	83.0[c]	118.4	159.4	186.4	235.3	251.0
5.4	54.3	86.4	121.1	159.7	188.0	236.5	251.7
5.5	54.4	86.6	121.4	161.1	190.0	239.0	253.0
10.3	55.7	86.8[b]	121.9	161.2	191.5	239.9	253.5[b]
10.5	56.3	87.3	122.0	161.7	191.6	240.4[c]	256.0
11.8	56.4	87.9	122.6	162.3	192.3	240.7	259.0
13.0	56.6	90.2	Quiver Lake[b]	163.0	193.1	241.0	260.2
13.2	57.5	91.5	125.0	164.5	193.5	241.5	262.6
14.9	57.6	92.6	125.5	165.1	193.6	242.9	263.7
15.0[b]	58.0	93.4	126.4	165.2	194.1	244.3	265.5
19.2	58.9	93.6	126.6	165.3	196.1[b]		265.7
19.4	60.8	94.3[b]	128.2	166.3	196.3[b]		268.2
20.6	62.4	95.6	129.5	166.6	197.2		268.7
21.7	62.6	95.8	129.8[b]	167.2[b]	198.1		272.0
24.4	63.8	96.8	130.4	167.7	199.3		
26.0	64.4	98.0	132.0	167.9	200.4		
27.9	66.4[b]	99.5	132.1	168.1	201.2		
28.9	66.5	100.5	135.0	168.2	202.1		
29.0	66.6	106.6	135.5	168.3	202.8		
30.5	66.9	106.7	140.5	168.6	203.4		
30.6	68.3	106.8[c]	140.9	168.9	204.0		
33.2	68.6	106.9	143.0	169.3	205.0		
33.3	68.9	107.5	143.7	169.5	206.0		
35.9	69.0	108.3	145.0	170.8	208.2		
37.3	69.4	109.0	145.7[b]	170.9	209.4		
39.2	70.8	110.0	147.3	173.0	210.7		
39.3	Meredosia Lake[b]	110.1	147.7	173.4	213.2		
40.3	72.0	112.0	147.8	174.1	213.4		
42.3	72.9	112.1	148.2	174.9	214.0		
44.9[c]	73.0	113.2	148.5	175.8	214.9		
45.3	73.3	113.3	149.4	177.4	217.4		
45.9	73.7	113.7	151.1	179.7	219.4[b]		
47.4	74.6	Lake Matanzas[b]	153.6	180.5	219.8		
47.5	75.8[b]	115.3	154.4	181.0	220.7		
48.3	78.4	115.5	154.5	181.3	223.0		
51.0	78.8	116.3	156.0[b]	182.3	224.0		
51.2	79.8	117.0	156.4	183.5	225.8		
53.6		117.1		184.1	228.3		
				184.5[b]	229.0		
				184.6	229.3		

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[a] Miles from the mouth of the Illinois River at Grafton, Illinois. If no footnote reference is given after a river mile number, collections were made only for living mussels.

[b] Collections were made here for both living mussels and old shells.

[c] Collections were made here only for old shells.

[d] One collection was made in Aux Sable River near its mouth.

the investigator more assurance of collecting a variety of species in a given locality than by sampling at random. The author believes that a combined series of such collections permits one to use the data with some confidence for comparative purposes with sample series from other parts of the river. For example, in the more polluted navigation pools of the Illinois River the author electrofishes (Fig. 3), on a unit-of-time basis, habitats that he believes should support various species of sunfishes (Centrarchidae) as well as other fishes. He usually takes only a few or none of the more desirable species, whereas in similar habitats of other navigation pools such species may occur abundantly. Such results clearly reflect the effects of pollution on fish life and show the cumulative effects of poor water quality on a stream's ecosystem, which may not be discernible through chemical and bacteriological analyses of the water. The author merely incorporated his fishing sampling techniques into the design of the 1966 mussel survey to determine the effects man has had upon the mussel fauna of the river. Furthermore, this sampling design fitted well into the management aspects of the survey, which were to determine the condition of known mussel beds and to locate new beds that might be of commercial importance.

Crowfoot Bar

Since 1897 (Smith 1899:294) the crowfoot bar, or brail, has been used widely in the Midwest as a commercial fishing device to collect mussels (Fig. 4). The commercial bar varies from 10 to 17 feet in length and may have as many as 200 hooks, or crowfeet (4-pronged hooks), attached to the bar by short lines or chains. After conversing with several commercial fishermen, the author decided to use a bar much shorter than the commercial bar. The short bar was easier to fish and enabled us to cover greater distances in less time than would have been possible using a commercial bar. Also, the short bar was quite versatile in fishing stumpy and narrow habitats. The short bar used in this study was the exploratory crowfoot bar designed by the Tennessee Shell Company for their fishermen to use in locating new fishing sites in the Midwest. Three

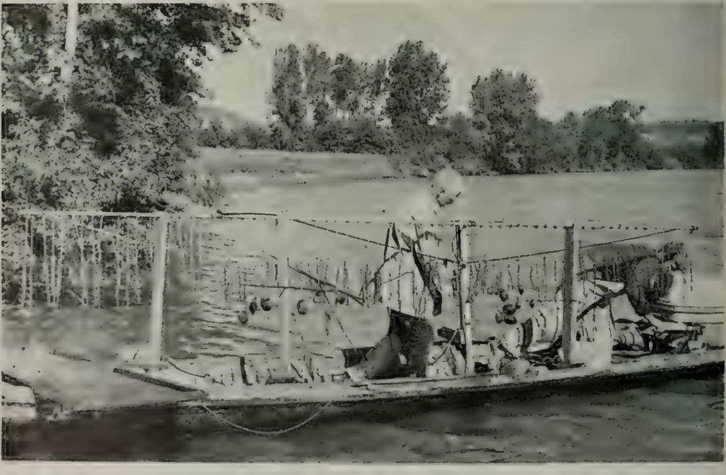

Fig. 4.—Typical crowfoot bar used by commercial mussel fishermen on the Illinois River in 1966. Photo by Alvin C. Lopinot.

of these bars were built for us by the Tennessee Shell Company. The bar was 61.25 inches long, and 44 hooks (0.1 inch in diameter) were suspended from the bar (Fig. 5).

A nylon towline was secured to either end of the bar, and the bar was fished from the bow of the boat. The boat was run in reverse, and all of the crowfoot bar fishing was done in a downstream direction. The bowman handled the bar and signaled the boat operator when the towline was played out and the bar commenced to fish. Upon noting this signal, the boat operator began timing the fishing with a stop watch. He also recorded on the field sheet the river depths and bottom types observed by the bowman while the bar was fishing (Table 3). The depths were taken

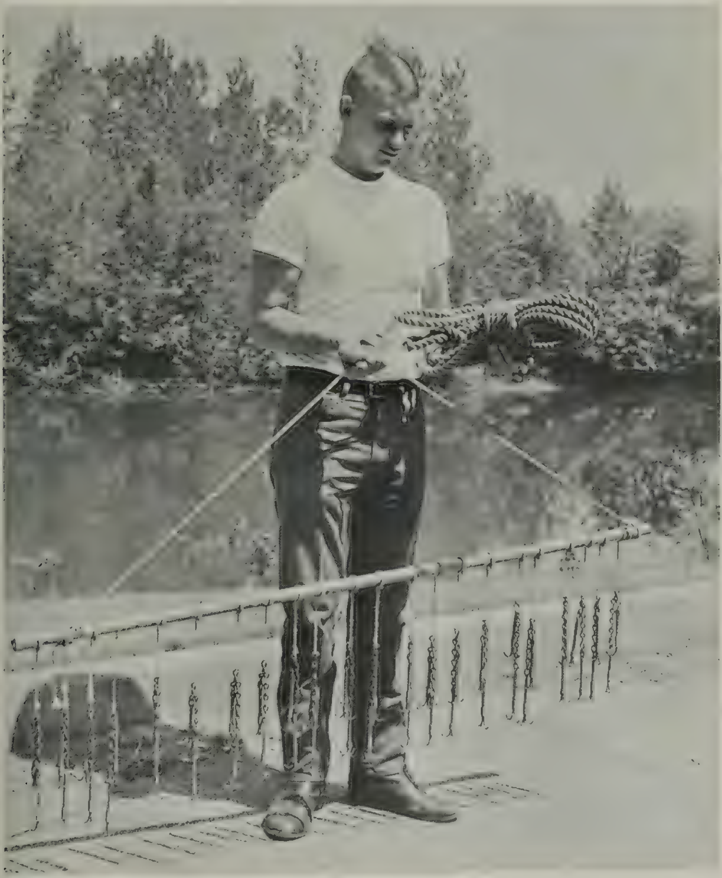

Fig. 5.—The exploratory crowfoot bar used on the Illinois River in the 1966 mussel survey. Photo by W. D. Zehr.

Table 3.—Average depths and depth ranges at which mussel collections were made with the crowfoot bar and dredge in the Illinois River in the 1966 survey.

Navigation Pool	*Crowfoot Bar*		*Dredge*	
	Average Depth in Feet	Depth Range in Feet	Average Depth in Feet	Depth Range in Feet
Alton	10.1	2.0–22.0	9.5	1.5–14.0
La Grange	10.8	2.5–18.0	8.9	2.0–14.0
Peoria	8.7	2.0–20.0	7.6	3.0–12.0
Starved Rock	7.9	2.0–14.0	...	...
Marseilles	9.0	1.5–14.5	...	...
Average Depth	*9.3*		*8.7*	

with a lead line, and the bottom types were determined from samples scooped from the bottom with a heavy collecting can mounted on the end of a long pole. According to Coker (1921:46–47):

> "When a hook enters a shell opening, the mussel closes firmly upon the hook, and in consequence is dragged from the bottom."

In some parts of the river it was necessary to raise the bar about every 200 or 300 feet to remove debris and/or live mussels from the hooks. As soon as the bowman began retrieving the bar or the bar became entangled, the boat operator stopped the timing record. By using a stop watch, it was possible to record the total fishing time expended for a collection, regardless of the number of times it was necessary to raise the bar (Table 4).

During the survey 322 collections were made with the crowfoot bar and 2,269 live mussels were taken. The first collection made at each selected fishing site (other than wading sites) was done on an exploratory basis with the crowfoot bar. Usually an exploratory collection was made on each side of the river at each sampling station. There were 229 exploratory crowfoot bar collections, and the distances covered in these runs average 1,390 feet (range, 300–5,280 feet). The water depths fished averaged 9.4 feet (range, 1.5–20 feet).

In addition to the exploratory fishing, 93 crowfoot bar collections were taken on a semiquantitative basis by fishing the bar over a measured distance of 400 feet. The semiquantitative collections were taken only at the stations where mussels had been taken earlier in the day in exploratory runs. The sampling area was marked off in a downstream direction by laying out 400 feet of nylon line attached at either end to anchored buoys. Small styrofoam floats at 100-foot intervals supported the line. The average depth of the water for all semiquantitative samples was 10.5 feet (range, 4.5–22.0 feet).

Two series of experiments demonstrated that the semiquantitative samples taken with the crowfoot bar were of no value in expressing the number of mussels present in the 400-foot area fished because of the inefficiency of the bar in collecting most of the live mussels present (regardless of size). The catches and number of crowfoot bar runs made in these two experiments were excluded from the other collections made in the

Table 4.—Number of mussels caught per 5 minutes of fishing with the experimental crowfoot bar over various types of bottoms in the Illinois River in 1966.

Bottom Type	*Number of Mussels Taken*		
	Alton Pool	La Grange Pool	Peoria Pool
Hard mud	11.2	2.4	0.1
Soft mud	5.7	0.7	0.1
Mud-gravel	6.4	0.0	0.2
Mud-sand	6.7	0.6	1.8
Sand	3.5	0.5	0.7
Gravel	0.0	0.0	0.5
Sand-gravel	1.4	0.2	16.5

survey and were not included in this paper.

Since all of the 322 regular crowfoot bar collections were made on a timed basis, the author combined collections from individual sections or navigation pools and expressed the catches as numbers of live mussels caught per 5 minutes of fishing (Tables 4 and A-4–A-8).

Dredge (Dip Net)

According to Danglade (1914:29–30):

> "Since the time that the mussel fishery began on this river [Illinois], it was known that Peoria Lake contained large beds of good commercial shells, but until 1911 no very successful method of taking them had been devised, scissor forks, oyster tongs, rakes, and the ordinary mussel bar with crow-foot hooks proving unsatisfactory. The dip net was introduced during the spring of that year and is now used there almost exclusively, as it is simple in construction, inexpensive, and especially suited to soft mud bottoms free from logs and hang-ups, and where there is but little or no current.
>
> * * *
>
> In a general way the dip net consists of a heavy, flattish iron hoop

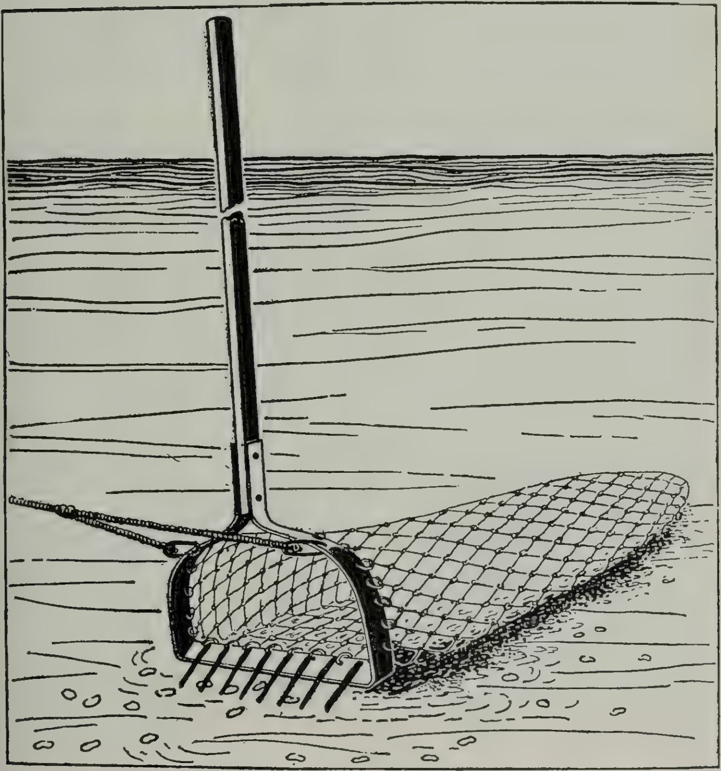

Fig. 6.—Sketch of a dredge fishing for mussels on the bottom of a river (from Danglade 1914:30).

of one piece, bent somewhat triangular in form, with two of its sides curved outward and fastened firmly with bolts to a pole or handle 16 to 20 feet long. The third side or bottom is straight and from 18 to 36 inches in length, and is usually provided with coarse teeth along its edge, which is bent downward. A net of 2-inch mesh, made of small chain or no. 96 trot line with a capacity of a bushel or more, is fastened to the hoop by means of chain links and trails behind it. A short

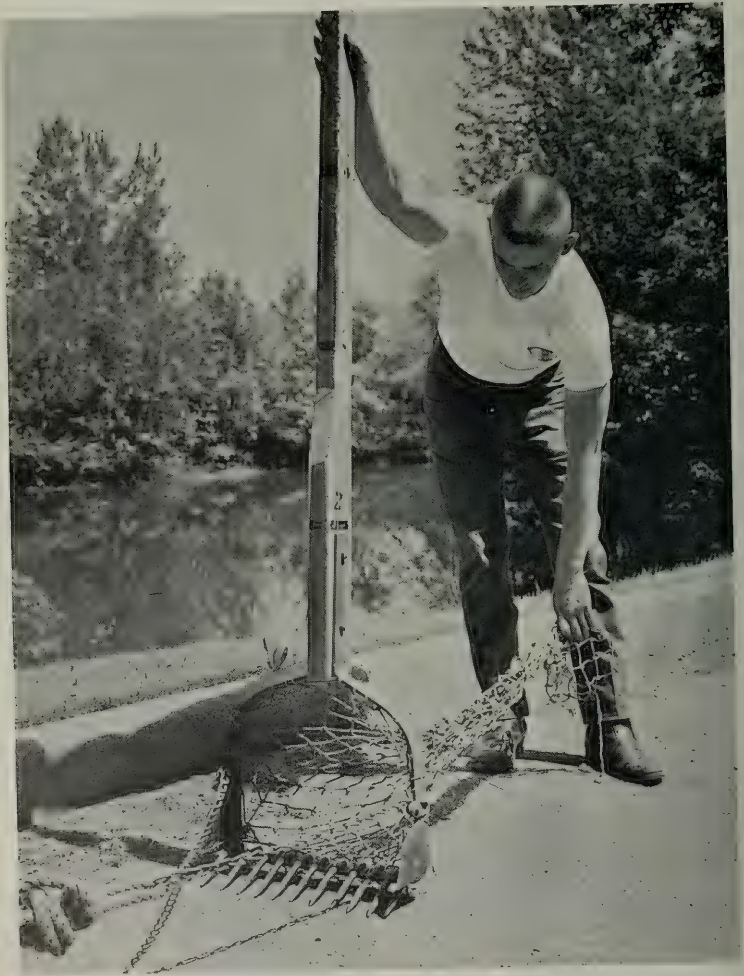

Fig. 7.—The dredge used in the Illinois River in the 1966 mussel survey. Photo by W. D. Zehr.

> rope or bridle attached to the two curved sides of the hoop leads to a single rope secured to the bow of the boat. When the water is rather deep, the boats are fitted with a boom pole extending forward from the bow, and the rope from the bridle is fastened to its end, thus giving greater length of rope and convenience of manipulation. Driven by a gasoline engine of from 4 to 20 horsepower, according to the size and weight of the dip net, the boat draws the apparatus through the water along the bottom" (Fig. 6).

The dip net, or dredge as it is now called by local fishermen, is still an important commercial mussel fishing device on the Illinois River. The dredge used in the 1966 survey (Fig. 7) was constructed by the Tennessee Shell Company. It was 14.75 inches wide and was attached to a pole 15.0 feet long. The pole was marked off in feet to enable the dredge operator to make water depth readings while fishing (Table 3). Our dredge was fished as described by Danglade by connecting the bridle of the dredge with a line to a wooden boom temporarily mounted on the bow of the boat (Fig. 8 and Tables A-4–A-8). The author considered this method of fishing very effective over the predominantly mud or mud-sand bottoms of the lower three navigation pools of the river. The bottom types of the upper river were not suitable for using the dredge.

In the survey 885 live mussels were taken in 74 dredge collections. In making these collections it was found that the dredge could be fished for only a very short distance or length of time (usually less than 1 minute) before it was necessary to raise it and clean out the net. This task was time consuming, since the entire net load of debris and dead shells had to be sorted through for live mussels before the collecting could be continued. This shortcoming of the dredge limited its use for us as an exploratory fishing device. Consequently, only 17 exploratory collections were made with the dredge and these were confined mainly to parts of Peoria Lake where, because of the almost nonexistent current, it was impractical to

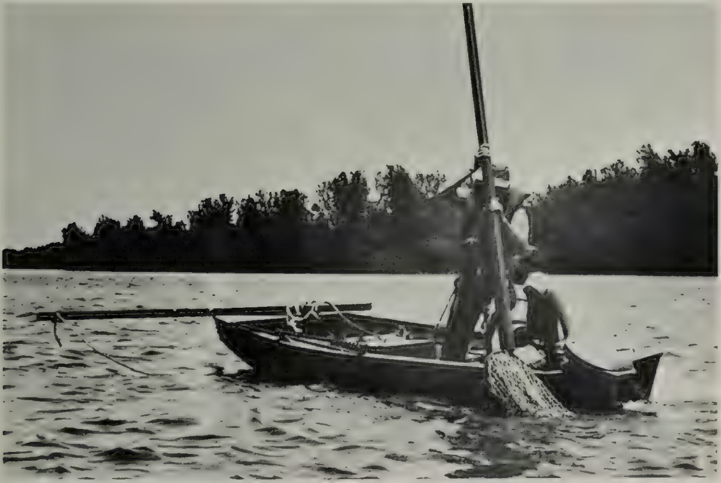

Fig. 8.—Lowering the dredge into the Illinois River during the 1966 mussel survey. Note the temporarily mounted boom on the bow of the boat to which the brail line was secured. From a color photo by the author.

fish the crowfoot bar. The average water depth fished in the dredge exploratory collections was 5.4 feet (range, 1.5–12.0 feet).

The dredge was used primarily for taking 57 quantitative samples of live mussels in the 400-foot marked sampling areas described above. In these collections the dredging was done on the side of the river opposite the 400-foot line fished with the crowfoot bar. The dredge appeared to be efficient in taking most of the live mussels in its path other than specimens less than 1.5 inches long and the mud-burrowing slough sand-shell (*Lampsilis anodontoides* f. *fallaciosa*). The average depth fished in the quantitative collections with the dredge was 9.8 feet (range, 5.0–14.0 feet).

Wading

Early in the program Dr. Paul W. Parmalee suggested that crowfoot and dredge collections should be supplemented with a series of wading collections to take small-sized mussels and species inhabiting shallow waters.

During the survey 33 different sites were sampled on a time basis by one to five men (usually three) wading in the river and grubbing the bottom with their hands for live mussels (Tables A-4–A-8). The water depths in the wading collections varied from 0.0 feet to 4.0 feet. In these collections 1,123 live mussels were taken.

Old Shells

Upon the suggestion of Dr. David H. Stansbery we collected old shells (subfossil) from 21 different locations along the river (Table 2). The purpose of these collections was to obtain specimens for verification of old records in the literature and information on the distribution of species formerly present in the river.

Commercial Shells

In the fall of 1966 commercial piles of mussel shells were examined at Meredosia and Kampsville along the Illinois River and at Mt. Carmel, Illinois, along the Wabash River. The shells were selected at random from sorted and culled commercial piles. In this phase of the study 1,937 shells were identified and measured (height to the nearest 0.1 inch) in the field and returned to the piles.

LABORATORY PROCEDURE

Live Mussel Shell Collections

Each field collection of shells was processed separately in the laboratory. The shells in each collection were identified, numbered, weighed, and measured; their ages were determined; and they were stored temporarily in plastic bags.

Tentative identifications of the shells were made by the author when each collection was sorted in the laboratory. Later, specimens representing each species taken in the survey together with complete series of certain species were submitted to Dr. David H. Stansbery for identification. As a result, most of the scientific names used here follow the nomenclature suggested by Stansbery (1961, 1962, and 1967). The nomenclature involving the various species known from the Illinois River is discussed in the next section of this paper.

The English system of weights and measurements was used by the author in this study because an important phase of the investigation dealt with the commercial and management aspects of the river's mussel fishery. However, metric system measurements made by Dr. Stansbery relative to the taxonomy of several species are included.

The shells in a collection were weighed individually by species on a Chatillon scale (0.01 pound).

Shell length and height measurements were made with a Helios dial caliper (0.01 inch). These measurements were made in accordance with Stansbery's definitions (1961:10):

> "LENGTH is the maximum antero-posterior dimension of the shell.
>
> "HEIGHT is the maximum dorsoventral dimension of the shell meas-

ured at right angles to the length. This dimension does not include the ligament, umbones nor the wing in the alate species, *Proptera alata* (Say) and *Leptodea fragilis* (Rafinesque)."

Ages of the mussels were determined by counting the number of annuli on the shells (Stansbery 1961:12–13). Usually both shells of a pair were used in making an age determination over a transmitted-light chamber. In some instances it was quite difficult to distinguish the true annuli from the false. However, the author believed that even though errors probably were made, the overall average age data for the more abundant species were accurate enough to be of value.

Specimens representing all of the species taken in the survey were deposited in The Ohio State Museum at Columbus, Ohio. Series of specimens of the more common species were deposited in the Field Museum of Natural History at Chicago, Illinois. The catalog numbers (OSM and FMNH) of these specimens have been listed for each species in the next section of this paper under the heading "Live Mussel Records (1966 Survey)." The remaining specimens were stored temporarily at the field laboratory of the Illinois Natural History Survey near Havana.

Estimated standing crops in pounds of live mussels and pounds of commercial shells per acre were calculated from the quantitative dredge collections:

1) Dredge width (1.23 feet) times the distance covered by the dredge in a collection (400 feet) equals the square feet sampled:

   $$1.23 \times 400 = 492$$

   number of square feet sampled

2) Square feet in an acre (43,560) divided by the number of square feet sampled in a collection equals the portion of an acre sampled:

   $$43{,}560 \div 492 = 88.54$$

   portion of an acre sampled

3) Live weight or commercial shell weight times the portion of an acre sampled equals the estimated standing crop in pounds per acre. For example,

   a) 16.72 pounds equals the live weight of mussels taken in a dredge collection at river mile 1.0

   b) $16.72 \times 88.54 = 1{,}480.39$, or 1,480 pounds
   estimated standing crop of live mussels in pounds per acre.

Old Shell Collections

The shells taken in the 1966 "bone" (subfossil) collections were identified by Dr. David H. Stansbery. The river mile numbers where old shells were collected and museum catalog numbers of the specimens deposited in The Ohio State Museum are included in the next section of this paper for each species under the heading "Old Shell Records (1966 Survey)."

Museum Collections

The author attempted to verify published records of those species previously reported from the Illinois River which were not taken in the 1966 live mussel and old shell collections. Verifications were made by curators at museums or by the author.

Dr. Paul W. Parmalee (pers. comm., 21 November 1966) furnished the author with copies of the accession pages of the Illinois State Museum at Springfield, Illinois, including mussels Dr. Parmalee had collected from the Illinois River in the 1950's. Dr. Henry van der Schalie (pers. comm., 31 August 1967) sent the author information relative to mussel shells from the Illinois River contained in the collections of the University of Michigan Museum of Zoology at Ann Arbor, Michigan. Dr. Joseph P. E. Morrison (pers. comm., 14 July 1967; 27 November 1967; 4 January 1968; 4 June 1968) provided records of mussels he collected from the

Illinois River in 1924 and the 1930's. He also provided information concerning mussels taken from the river by the U.S. Bureau of Fisheries from 1907 to 1916 and by others and now deposited at the U.S. National Museum at Washington, D.C. Dr. William J. Clench (pers. comm., 12 August 1969; 25 November 1969) furnished the author records of the Illinois River mussel shells in the collections of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Several of the shells in this collection were examined for the author by Dr. David H. Stansbery (pers. comm., 20 January 1970; 13 February 1970). Dr. Stansbery sent the author a list of the Illinois River naiads contained in the collections of The Ohio State Museum at Columbus, Ohio (pers. comm., 22 December 1969).

Dr. Lowell Getz, while at the University of Connecticut (now at the University of Illinois), presented the author with some of the shells contained in the Benjamin Koons collection from the Illinois River in the 1870's. The author gave several of these shells to Dr. Paul W. Parmalee for deposit in the Illinois State Museum. The remainder of these shells will be presented to the Illinois Natural History Survey at Urbana, Illinois, and The Ohio State Museum.

The author examined mussels from the Illinois River in the collections of the following museums: Field Museum of Natural History at Chicago, Illinois; University of Illinois Museum of Natural History (Frank C. Baker collection) at Urbana, Illinois; and Illinois Natural History Survey at Urbana, Illinois.

Abbreviations of the names of the museum and personal collections consulted during the preparation of this paper are: Benjamin Koons collection (BK), Field Museum of Natural History (FMNH), Illinois Natural History Survey (INHS), Illinois State Museum (ISM), Museum of Comparative Zoology (MCZ), The Ohio State Museum (OSM), U.S. National Museum (USNM), University of Illinois Museum of Natural History (UIMNH), and University of Michigan Museum of Zoology (UMMZ).

MUSSEL FAUNA OF THE ILLINOIS RIVER

This section deals with the past and present mussel fauna of the river. Through the years various generic and specific names have been used by different authors for a number of the mussel species found in the Illinois River. Differences in opinions among taxonomists concerning the nomenclature of many of these species still exist and will probably continue to exist until the evidence for solving the many problems is obtained. In this paper the author was more concerned with presenting a synoptic report of the mussel fauna of the river which might be intelligible to current and future workers than with the problems of taxonomy and nomenclature.

Persons desiring to identify mussels from the Illinois River will find Parmalee's (1967) booklet on the mussels of Illinois very helpful. To aid such persons the author has included with the synonymies of most of the species listed below pertinent references to Parmalee's publication and the scientific names used by him. Otherwise, the synonymies include only those names referring to Illinois River records appearing in the literature and personal communications and those found on museum specimens.

For the benefit of those having a serious interest in the Illinois mussel fauna the author has included at the end of the discussion of each species three categories of mussels collected from the Illinois River: (i) "Museum Records," specimens not collected in the 1966 survey; (ii) "Live Mussel Records (1966 Survey)," the Illinois River mile number and river bank and/or the name of the bottomland lake where living specimens were collected in 1966 and their museum catalog numbers (mussels collected alive from the Peoria pool in 1969 were included here and designated as 1969 records); and (iii) "Old Shell

Table 5.—Mussel fauna of the Illinois River and its bottomland lakes in the 1870-1900 period, 1906-1912 period, and 1966-1969 period.[a]

Kind of Mussel	*Period*		
	1870–1900	1906–1912	1966–1969[b]
Cumberlandia monodonta (Spectacle-Case)	P[c]	P	A
Fusconaia ebena (Ebony Shell)	P	P	P
Fusconaia flava f. *flava* (Wabash Pig-Toe)	P	P	A
Fusconaia flava f. *undata* (Pig-Toe)	P	P	P
Megalonaias gigantea (Washboard)	P	P	P
Amblema plicata (Three-Ridge)	P	P	P
Quadrula quadrula (Maple-Leaf)	P	P	P
Quadrula pustulosa (Pimple-Back)	P	P	P
Quadrula nodulata (Warty-Back)	P	P	P
Quadrula metanevra (Monkey-Face)	P	P	A
Tritogonia verrucosa (Buckhorn)	P	P	P
Cyclonaias tuberculata (Purple Warty-Back)	P	P	A
Plethobasus cyphyus (Bullhead)	P	P	A
Pleurobema coccineum f. *solida*	P	P	A
Pleurobema pyramidatum	P	P	A
Elliptio crassidens (Elephant's Ear)	P	P	A
Elliptio dilatatus (Lady-Finger)	P	P	A
Uniomerus tetralasmus (Pond-Horn)	P	A	A
Arcidens confragosus (Rock Pocketbook)	P	P	P
Lasmigona costata (Fluted Shell)	P	P	A
Lasmigona complanata (White Heel-Splitter)	P	P	P
Anodonta grandis grandis (Floater)	P	P	P
Anodonta grandis corpulenta (Floater)	P	P	P
Anodonta imbecillis (Paper Pond Shell)	P	P	P
Anodonta suborbiculata (Heel-Splitter)	P	P	P
Alasmidonta calceolus (Slipper-Shell)	P	A	A
Alasmidonta marginata (Elk-Toe)	P	A	A
Strophitus undulatus (Squaw Foot)	P	P	A
Anodontoides ferussacianus (Cylindrical Paper Shell)	P	P	A
Obliquaria reflexa (Three-Horned Warty-Back)	P	P	P
Obovaria olivaria (Hickory-Nut)	P	P	P
Actinonaias ligamentina (Mucket)	P	P	A
Plagiola lineolata (Butterfly)	P	P	A
Truncilla truncata (Deer-Toe)	P	P	P
Truncilla donaciformis (Fawn's Foot)	P	P	P
Leptodea fragilis (Fragile Paper Shell)	P	P	P
Proptera alata (Pink Heel-Splitter)	P	P	P
Proptera capax (Fat Pocketbook)	P	P	A
Proptera laevissima (Fragile Heel-Splitter)	P	P	P
Carunculina parva (Liliput Shell)	P	P	P
Ligumia recta (Black Sand-Shell)	P	P	A
Villosa iris iris (Rainbow-Shell)	P	A	A
Lampsilis anodontoides f. *anodontoides* (Yellow Sand-Shell)	P	P	A
Lampsilis anodontoides f. *fallaciosa* (Slough Sand-Shell)	P	P	P
Lampsilis radiata luteola (Fat Mucket)	P	P	P
Lampsilis ventricosa (Pocketbook)	P	P	A
Lampsilis orbiculata f. *orbiculata*	P	P	A
Lampsilis orbiculata f. *higginsii* (Higgin's Eye)	P	P	A
Dysnomia triquetra (Snuffbox)	P	P	A

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[a] Doubtful records of occurrence in the 1870-1912 period: *Margaritifera margaritifera; Fusconaia subrotunda; Lastena lata; Lasmigona compressa; Obovaria retusa;* and *Leptodea leptodon.* Recorded from the Illinois River valley: *Ligumia subrostrata.*

[b] Includes only mussels taken alive in the 1966-1969 study.

[c] P designates present; A designates absent.

Records (1966 Survey)," the Illinois River mile where subfossil shells of the species were collected in 1966 and their museum catalog numbers.

Phylum MOLLUSCA
Class PELECYPODA
Order EULAMELLIBRANCHIA
Superfamily UNIONACEA
Family MARGARITIFERIDAE
Ortmann, 1911

Margaritifera margaritifera
(Linnaeus, 1758)

Margaritana margaritifera Linné:
Baker (1906:76)

Baker (1906:76) reported that Calkins collected this species in the Illinois River. The author was unable to locate a specimen of this species from the Illinois River in the museums he visited or contacted during this study.

This species apparently is restricted largely to soft waters and is usually found in cold, clear, rather rapidly flowing small to medium-sized streams (Ortmann 1919:5; Clarke & Berg 1959:18). According to Clarke & Berg (1959:17) this species has not been collected from central North America. The Illinois River is a large, sluggish, hard-water stream located virtually in the heart of central North America.

On the basis of this evidence the author concluded that Baker's reporting of *M. margaritifera* in the Illinois River was an error and that this species should not be included in the mussel fauna list of the river presented in Table 5.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Spectacle-Case
Cumberlandia monodonta (Say, 1829)

Cumberlandia monodonta (Say):
Parmalee (1967:25)
Margaritana monodonta Say
(=*soleniformis* Lea):
Baker (1906:76)
Margaritana monodonta (Say):
Danglade (1914:10)

The spectacle-case was listed by Baker (1906:76) as having been taken at Havana, Illinois, by State Laboratory personnel. Also Danglade (1914:42) mentioned that he saw several specimens of this species from the Illinois River at the biological laboratory at Havana. A single specimen of the spectacle-case was collected in 1912 by Danglade (Ibid.) from the river at Diamond Island (approximate river mile 24.5) above Hardin. Dr. Joseph P. E. Morrison (pers. comm., 14 July 1967; 27 November 1967) confirmed this record (USNM).

Danglade (1914:42) reported that the spectacle-case was a rare species in the Illinois River in 1912. This species was probably similarly scarce in the Mississippi River where the van der Schalies (1950:456) listed the spectacle-case as occurring so rarely in the mainstream that collecting a specimen was merely a matter of chance.

Neither a living nor a subfossil spectacle-case was taken in the 1966 survey. Nor was this species collected by Parmalee (pers. comm., 29 June 1967) during the 1950's from the Illinois River. It appears that the spectacle-case has disappeared from the river in the past 50 years. Stansbery (1966:29) reported a similar disappearance of this species from the Ohio River.

Museum Records.—Above Hardin, Diamond Island (1912 Danglade) USNM 678486.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Family UNIONIDAE (Fleming, 1828)
Ortmann, 1911

Subfamily UNIONINAE (Swainson, 1840) Ortmann, 1910

Ebony Shell
Fusconaia ebena (Lea, 1831)
(Plate 3-18)

Fusconaia ebenus (Lea):
Parmalee (1967:31; 1962:9)

Unio ebenus Lea:
  Calkins (1874:42)
Quadrula ebena Lea:
  Kelly (1899:401)
  Baker (1906:81)
  Forbes & Richardson (1913:536)
Quadrula ebena (Lea):
  Danglade (1914:9)
Fusconaia ebena:
  Richardson (1928:457)
Sintoxia antrosa Raf., 1820:
  Morrison (pers. comm., 4 January 1968)
Fusconaia antrosa (Raf.):
  FMNH

Danglade (1914:38) considered this species as the most valuable button shell in the United States. He stated that:

> "Although widely distributed throughout the entire river [Illinois], this species is so rare in the upper stretches that often only one or two examples are found in a ton of shells. In the lower third of the river the conditions are better; the number may run as high as 2 or 3 per cent."

In the early 1870's Calkins (1874:42) found the ebony shell occurring abundantly in the river at La Salle County (Starved Rock pool). Baker (1906:81) reported this species from the river at Utica and Havana. In the 1896-1897 period, Kelly (1899:401) examined 23 specimens of ebony shells collected in the Havana area.

In 1912 Forbes & Richardson (1913:536) collected live ebony shells in the river between Chillicothe and Henry. However, in the 1924-1925 period Richardson (1928:457) was unable to find a living specimen of this species in Peoria Lake.

Morrison (pers. comm., 4 January 1968) collected this species in the river at Meredosia in 1930, and in 1955 Parmalee (pers. comm., 21 November 1966) took one live ebony shell at Naples.

Only one living specimen of this species was taken in the 1966 survey. This mussel was collected near the mouth of the river with the crowfoot bar on a hard bottom in 9.0 feet of water. The height of the specimen was 2.8 inches, and it was determined to be 14 years old. This species was not found in the Illinois River commercial shell piles examined in 1966.

Formerly, the ebony shell was a fairly abundant mussel in the Illinois River as evidenced by the records presented here. Today it is rare and apparently occurs only in the lower part of the river (Alton pool). This virtual disappearance of the ebony shell from the Illinois River during the past 50 years probably was related to siltation and pollution rather than to any change in the fish population. The known fish host for this mussel (Baker 1928:67), the skipjack herring, *Alosa chrysochloris* (Rafinesque), has always been considered an uncommon species in the Illinois River (Forbes & Richardson 1920: 49; Starrett & Smith unpublished).

Museum Records.—Chillicothe (1907 Freeland & Williams) USNM 676962; Havana area (pre-1900 Strode) FMNH 9220 and 50574, (1894) UIMNH 22179, and (1909) INHS; Meredosia (1907 F & W) USNM 676951 and (1930 Morrison) USNM 678633; Naples (1955 Parmalee) ISM 1122; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678555; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678556; and Illinois River without locality (pre-1943 Webb Coll.) FMNH 22845.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB). OSM 18013.

Old Shell Records (1966 Survey).—River mile 15.0, 44.9, 66.0–66.4, 75.8, 86.6, 94.3, 106.8, 129.8, 145.7, 156.0, 196.3, 198.1, and 219.4. OSM 18194, 18207, 18251, 18276, 18289, 18311, 18327, 18357, 18441, and 18452.

Fusconaia subrotunda (Lea, 1831)

Fusconaia subrotunda (Lea):
  Parmalee (1967:87)
Quadrula subrotunda Lea:
  Baker (1906:81)

Baker (1906:81) stated that *F. subrotunda* was reported from the Illinois

River by Call. The author was unable to locate a specimen of this species taken from the Illinois River. According to Simpson (1914:893) this species occurred in the Ohio, Cumberland, and Tennessee river systems. Parmalee (pers. comm., 29 June 1967) informed the author that:

> "I have never collected this in the Illinois River or in any river in the state, for that matter. Apparently this species is confined to the Ohio River and its tributaries and if it still occurs there today, it would be rare."

Van der Schalie (pers. comm., 31 August 1967) considered the Illinois River out of the range for this species. Morrison (pers. comm., 27 November 1967) mentioned that any records of this species from the Illinois River were probably misidentified (flatter) specimens of ***F. ebena***.

On the basis of the evidence the author has excluded this species from his mussel fauna list of the Illinois River (Table 5).

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Fusconaia flava Complex

A series of specimens belonging to the *Fusconaia flava* complex collected from the river in the 1966 survey was submitted to Dr. David Stansbery for examination. The comments and analysis made by Dr. Stansbery (pers. comm., 12 July 1967) concerning this complex and the Illinois River material were:

> "A total of 29 specimens of this form constitute our holdings of this species from the Illinois River. All but a single specimen were collected by Dr. William Starrett in 1966 and these latter specimens comprise 14 separate lots. These lots extend from Illinois River mile 1 to Ill. Riv. mi. 169.3.
>
> "Each specimen was measured as to length, height, and width. A vernier caliper was used and each dimension rounded off to the nearest millimeter. From these data were calculated the height index $\left(\frac{H}{L} \times 100\right)$, width index $\left(\frac{W}{L} \times 100\right)$, and transverse index $\left(\frac{W}{H} \times 100\right)$. It was the width index which Ortmann (1918, 1919, & 1920) used to differentiate the headwater forms from the downstream forms in a number of other species.
>
> "In order to work with this complex in Lake Erie (some years ago) I compared these same proportions of the holotypes of each of the described names in this complex. I found that (Stansbery 1960:104) there was a gradual gradation in both height and width indices from the very compressed *flava* Rafinesque, 1820, through *rubiginosa* Lea, 1829; *parvula* Grier, 1918; *trigonus* Lea, 1831; *undatus* Barnes, 1823; to *wagneri* Baker, 1928. The latter is the very high, very wide extreme found (then) in Lake Pepin of the Mississippi River. While I dislike to disagree with a worker of Baker's stature I must, in all honesty, confess that my concept of this group does not concur with his. I cannot separate any of the above described forms into species distinct from the first described — *flava* Rafinesque, 1820.
>
> "Since receiving this fine set of material from the Illinois River I have once again gone over my original measurements and calculations as well as the extensive material which has accumulated here at the Ohio State Museum in the interim. All of this has served only to convince me that the concept I arrived at in 1960 is the correct one. Had Baker had at his disposal the material we have for study today I

believe he would concur with the following arrangement.

	Width Index
Fusconaia flava forma *flava* (Raf., 1820)	Up to 54*
Fusconaia flava forma *undata* (Barnes, 1823)	55* and over

* see Ortmann 1920:282

"The names *flava* Raf. and *undata* Barnes are used above since they are conspecific and represent the earliest names applied to the compressed and swollen forms, respectively. Ortmann in some instances used a third designation for intermediate specimens. If for any reason this becomes desirable, the form *trigona* Lea lies intermediate between the extremes of this complex. Wherever I have had the opportunity to study all the *F. flava* forms within a single stream system it has proved to be a cline from *F.* f. *flava* in the headwaters to *F. f.* f. *undata* downstream.

"Whether the differences observed between the headwaters and the big rivers are principally genetic or environmental is not presently known and constitute a different, though not less interesting, problem.

"This brings us to the question of the identification of the Illinois River *Fusconaia flava* specimens. The width indices of the 29 specimens studied varied from a low of 57 to a high of 75 thus placing all of them in the form *undata*. A larger sample might well produce some form *flava* specimens and it's almost certain that collecting in the tributaries would do so. The mean width index for all 29 specimens was 66. This means that *Fusconaia flava* of the Illinois River proper groups with those forms found in the Mississippi River below Minneapolis, the lower Ohio River, lower Wabash River, and the lower White, Black, and St. Francis Rivers of Arkansas. There are a few records of this form of *F. flava* for the lower Cumberland and Tennessee Rivers (in Kentucky) but neither this form nor the compressed *flava* seem to have been able to invade the Cumberland Plateau or southern Appalachians. Related forms are present in the Gulf Coast rivers of the coastal plain from the Alabama River west to at least the Sabine River of Texas but apparently represent different species."

As Stansbery mentions, he was unable to separate the forms of *flava* discussed here into distinct species. However, van der Schalie (pers. comm., 31 August 1967) considered *flava* and *undata* to be separate species unless they were proved to be clines. Morrison (pers. comm., 27 November 1967) also treated *flava* and *lateralis* (*undata*) as separate species. The author has followed Stansbery's opinion relative to the *F. flava* complex and believes that the synonymies included below for each form will enable the reader to comprehend the form or species discussed, regardless of his opinion concerning this complex.

Wabash Pig-Toe

Fusconaia flava forma flava
(Rafinesque, 1820)

Fusconaia flava (Raf.):
  Parmalee (1967:31)
  FMNH
  MCZ
Unio rubiginosus Lea:
  Calkins (1874:44)
Quadrula rubiginosa Lea:
  Kelly (1899:401)
Quadrula rubiginosa (Lea):
  Danglade (1914:9)
Quadrula rubiginosa Lea (=*flava* Conrad):
  Baker (1906:80)

This headwaters and creek form of *Fusconaia flava* was not collected from the Illinois River in the 1966 survey. During the 1966 survey a living specimen of the creek form *flava* was taken in the Aux Sable River, a tributary stream of the upper Illinois River (OSM 17342).

Calkins (1874:44) considered *rubiginosus* an abundant species in the Illinois (Starved Rock pool) and Fox rivers. Downstream from Starved Rock at Peru several specimens of *F. flava* were collected from the Illinois (pre-1910) and later deposited in the Museum of Comparative Zoology. Dr. Stansbery (pers. comm., 20 January 1970) examined these museum specimens for the author and informed him that:

> "The *F. flava* I would term form *flava* Raf. but have the suggestion of the form *trigona* Lea which is one of several inter-connecting forms between *flava* Raf. and *undata* Barnes. They do not, however, have the outline, width index, high beaks or sulcus typical of *undata* Barnes."

Kelly (1899:401) indicated that in the 1896-1897 period he checked for parasites one specimen of this form from the river at Havana. Also Baker (1906:80) reported that *rubiginosa* was taken at Havana (no mention of stream) by State Laboratory personnel. The author examined in the collections of the Field Museum of Natural History a shell collected at Havana (no mention of stream) in 1895 which he considered to be form *flava*. The Illinois River flows past the west side of Havana, but directly across from Havana, Spoon River empties into the Illinois. The author conjectured that this shell was collected either in or near the mouth of Spoon River.

Danglade (1914:39) considered *rubiginosa* rare in the Illinois River, and the only examples of this mussel found in his survey were taken from Peoria Lake. Stansbery mentioned above that a larger sample in 1966 of *F. flava* f. *undata* from the river might have produced some specimens of the form *flava* and possibly Danglade's (Ibid.) records of this form (*rubiginosa*) were a result of examining large collections of specimens belonging to this complex. The tributary streams emptying into Peoria Lake were all temporary or intermittent creeks and were not typical streams where the form *flava* might be expected to occur. In the author's opinion the records cited above of form *flava* (*rubiginosus* and *rubiginosa*) occurring in the Illinois, other than Peoria Lake, were based on specimens collected at or near the mouths of tributary streams.

The host fish of this form is not known.

Museum Records.—Peru (pre-1910) MCZ 269572; and Havana, no stream mentioned (1895 Hay) FMNH 14898.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Pig-Toe
Fusconaia flava forma undata
(Barnes, 1823)
(Plate 3-14)

Fusconaia undata (Barnes):
  Parmalee (1967:32)
  Richardson (1928:457)
Unio trigonus Lea:
  Calkins (1874:45)
Quadrula trigona Lea:
  Kelly (1899:401)
  Forbes & Richardson (1913:533)
Quadrula trigona (Lea):
  Danglade (1914:9)
Quadrula undata (Barnes):
  Danglade (1914:39)
Fusconaia undata undata Barnes:
  FMNH
Fusconaia undata wagneri (Baker):
  FMNH
Fusconaia undata:
  Richardson (1928:457)
Sintoxia lateralis Raf., 1820:
  Morrison (pers. comm., 4 January 1968)

Danglade (1914:39) considered this form the most abundant of the "pig-toe" group in the Illinois River and stated that:

> "Some beds, depending upon the parts worked, gave the following percentages: Chillicothe, 7; Pekin, 3; Florence, 9; and Hardin, 2."

In the 1966 survey 46 live specimens of this form were taken between river miles 1.0 and 170.9 (Table A-3). The pig-toe constituted 1.1 percent of the live mussels taken in the survey and ranked 11th in abundance in the 1966 collections (Tables 6 and 7). The average height of these shells was 1.9 inches. Most of these shells were between 8 and 12 years of age (Table A-9). No pig-toe taken in the survey or examined in the Illinois River commercial piles was over 2.4 inches in height (minimum commercial height 2.5 inches). The small size and scarcity of this form in the Illinois River in 1966 virtually eliminated it as a commercial shell.

Formerly the pig-toe was distributed throughout most of the river, as indicated in the museum records and by subfossil shells found in 1966. In the 1966 survey neither a living nor an old shell of this form was taken in the Starved Rock navigation pool; however, Calkins (1874:45) reported it from this pool in La Salle County.

In the present study 26 live specimens were taken in the Alton pool and 19 specimens from the lower part of the Peoria pool. Only a single live pig-toe was collected in the La Grange pool (between Alton and Peoria pools). In the 1896-1897 period Kelly (1899:401) took 22 pig-toes from the river at Havana in the La Grange pool. In 1912 Forbes & Richardson (1913:533 & 536) collected pig-toes between Hennepin and Chillicothe. However, in the 1924-1925 period Richardson (1928:457) did not take this form above the lower end of Upper Peoria Lake. This was approximately the same upstream location (river mile 170.9) where live pig-toes dropped out of the 1966 survey collections.

According to Baker (1928:61) the white crappie, *Pomoxis annularis* Rafinesque, and black crappie, *Pomoxis nigromaculatus* (Lesueur), were believed to be the host fishes for the glochidia of the pig-toe. Both of these species, particularly the black crappie, were common

Table 6.—Rankings of the relative abundance of kinds of live mussels taken in the 1966 survey of the Illinois River and its bottomland lakes, based on the number of specimens collected.[a]

Kind of Mussel	*Alton Pool Rank*	*La Grange Pool Rank*	*Peoria Pool Rank*	*Entire River Rank*
A. plicata (Three-Ridge)	1	1	1	1
Q. pustulosa (Pimple-Back)	2	7	. .	2
Q. quadrula (Maple-Leaf)	3	2	3	3
M. gigantea (Washboard)	4	4	10	4
A. g. corpulenta (Floater)	8	3	2	5
A. confragosus (Rock Pocketbook)	6	6	10	6
Q. nodulata (Warty-Back)	5	10	. .	7
L. fragilis (Fragile Paper Shell)	9	5	7	8
L. a. f. fallaciosa (Slough Sand-Shell)	10	9	5	9
O. reflexa (Three-Horned Warty-Back)	7	12	. .	10
F. f. f. undata (Pig-Toe)	11	12	4	11
P. laevissima (Fragile Heel-Splitter)	12	8	6	12
P. alata (Pink Heel-Splitter)	13	12	8	13
L. complanata (White Heel-Splitter)	15	10	8	14
T. truncata (Deer-Toe)	14	11	. .	15
L. r. luteola (Fat Mucket)	. .[b]	11	7	16
A. imbecillis (Paper Pond Shell)	16	11	10	17
A. g. grandis (Floater)	. .	11	9	18
F. ebena (Ebony Shell)	17	. .	. .	19
A. suborbiculata (Heel-Splitter)	. .	12	. .	19
O. olivaria (Hickory-Nut)	17	. .	. .	19
T. donaciformis (Fawn's Foot)	17	. .	. .	19
C. parva (Liliput Shell)	17	. .	. .	19

[a] 1969 data are not included in this table.
[b] Mussel was not collected.

Table 7.—Rankings of the relative abundance of kinds of live mussels taken in the 1966 survey of the Illinois River and its bottomland lakes, based on the percentage of collections in which a kind of mussel occurred.[a]

	Alton Pool		*La Grange Pool*		*Peoria Pool*		*Entire River*	
Kind of Mussel	Percent of Collections in Which Mussel Occurred	Rank	Percent of Collections in Which Mussel Occurred	Rank	Percent of Collections in Which Mussel Occurred	Rank	Percent of Collections in Which Mussel Occurred	Rank
A. plicata (Three-Ridge)	78.4	1	40.8	1	39.5	1	54.4	1
Q. quadrula (Maple-Leaf)	56.8	3	31.5	2	10.9	4	34.8	2
Q. pustulosa (Pimple-Back)	59.5	2	6.2	7	0.0	..	24.2	3
M. gigantea (Washboard)	43.9	4	10.8	4	0.8	10	20.2	4
A. g. corpulenta (Floater)	8.1	7	10.0	5	20.2	2	12.3	5
L. fragilis (Fragile Paper Shell)	16.9	6	12.3	3	4.2	6	11.6	6
A. confragosus (Rock Pocketbook)	20.9	5	7.7	6	0.8	10	10.6	7
Q. nodulata (Warty-Back)	20.9	5	3.8	9	0.0	..	9.1	8
L. a. f. fallaciosa (Slough Sand-Shell)	6.8	8	4.6	8	11.8	3	7.6	9
F. f. f. undata (Pig-Toe)	8.1	7	0.8	11	10.9	4	6.5	10
O. reflexa (Three-Horned Warty-Back)	16.9	6	0.8	11	0.0	..	6.5	10
P. laevissima (Fragile Heel-Splitter)	4.1	10	4.6	8	5.0	5	4.5	11
L. complanata (White Heel-Splitter)	2.7	11	3.8	9	2.5	8	3.0	12
P. alata (Pink Heel-Splitter)	5.4	9	0.8	11	2.5	8	3.0	12
T. truncata (Deer-Toe)	4.1	10	1.5	10	0.0	..	2.0	13
L. r. luteola (Fat Mucket)	0.0	..	1.5	10	3.4	7	1.5	14
A. g. grandis (Floater)	0.0	..	1.5	10	1.7	9	1.0	15
A. imbecillis (Paper Pond Shell)	1.4	12	0.8	11	0.8	10	1.0	15
F. ebena (Ebony Shell)	0.7	13	0.0	..	0.0	..	0.3	16
A. suborbiculata (Heel-Splitter)	0.0	..	0.8	11	0.0	..	0.3	16
O. olivaria (Hickory-Nut)	0.7	13	0.0	..	0.0	..	0.3	16
T. donaciformis (Fawn's Foot)	0.7	13	0.0	..	0.0	..	0.3	16
C. parva (Liliput Shell)	0.7	13	0.0	..	0.0	..	0.3	16

[a] 1969 data are not included in this table.

in some years (1957–1967) in the Illinois River from its mouth to the Starved Rock dam and uncommon in the Starved Rock and Marseilles pools (Starrett unpublished). The decrease in abundance and distribution of the pig-toe in the Illinois River during this century probably was a result of pollution. Also, pollution has affected the fish hosts of the pig-toe, particularly in the upper two navigation pools of the river.

Museum Records.—Peru (pre-1943 Webb Coll.) FMNH 22829; Spring Valley (1924 Morrison) USNM 678631 (dead); Chillicothe (1907 Freeland & Williams) USNM 677037; Peoria (pre-1943 Webb Coll.) FMNH 22824; Pekin (1907) FMNH 11216; 3 miles SE of Banner (1953 Parmalee) ISM 220 (dead); Quiver Lake (1955 Parmalee) ISM 1049; Havana (1894 Baker) UIMNH 22171; Beardstown (1907 F & W) USNM 676954; Meredosia (1907 F & W) USNM 677026 and (1930 Morrison) USNM 678632 (dead); Naples (1955 Parmalee) ISM 1123; Valley City (1909 Freeland) USNM 678591; Pearl (1965 Parmalee) ISM 3310–3311; 1 mile below Hardin (1907) USNM 678554; and Illinois River without locality FMNH 57524 and (1870's) BK.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 10.5 (RB), 14.9–15.1 (RB), 28.9–29.1 (RB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 66.0–66.4 (LB), 73.0 (RB), 75.8 (RB), 154.4–154.5 (RB), 162.3 (LB), 166.6 (LB), 167.2 (LB), 167.2 (RB), 167.7 (LB), 168.1–168.5 (RB), 168.6 (LB), 169.3 (RB), and 170.9 (RB). OSM 17344, 17697, 17698 (2), 17699, 17713, 17714 (6), 17728 (5), 17729 (2), 17731 (3), 17732, 17735, 17736 (2), 17737, and 17738; FMNH 156957 (3) and 156966.

Old Shell Records (1966 Survey).—River mile 44.9, 66.0–66.4, 75.8, 94.3, 106.8, 129.8, 145.7, 156.0, 184.5, 196.1, 196.3–198.1, 219.4, 253.5–256.5. OSM 18193, 18277, 18288, 18310, 18326, 18356, 18381, 18429, 18440, 18451, and 18476.

Washboard

Megalonaias gigantea (Barnes, 1823)
(Plate 1-4)

Megalonaias gigantea (Barnes):
Parmalee (1967:33; 1962:9)
Richardson (1928:457)
MCZ
Quadrula multiplicata Lea:
Kelly (1899:401)
Quadrula heros Say
(=*multiplicata* Lea):
Baker (1906:78)
Forbes & Richardson (1913:533)
Quadrula heros (Say):
Danglade (1914:10)
Amblema (Megalonaias) gigantea gigantea (Barnes):
FMNH
Megalonaias gigantea Barnes:
Morrison (pers. comm., 4 January 1968)

Danglade (1914:40) considered the washboard the best button shell found in the Illinois River. In 1966 this species was the second most important shell taken from the Illinois River for use in the Japanese pearl-culture industry. The washboard ranked fourth in abundance in the 1966 survey collections (Tables 6 and 7) and constituted 4.9 percent of the live shells taken (Table A-3). Most of the washboards collected were over 2.5 inches in height (Table A-10) and 70.5 percent of them were between 11 and 18 years of age (Table A-11).

In 1912 the washboard was an abundant shell in various parts of the river between Spring Valley (river mile 218.5) and its mouth (Danglade 1914:13–24; Richardson 1928:457). Baker (1906:78) stated that this species had been taken from the river at Ottawa (river mile 239.5) and Utica (river mile 229.6). These citations from the literature together with the museum and subfossil shell records indicated that the washboard formerly was distributed throughout the river upstream as far as Ottawa. No record was located relative to the occurrence of the washboard in the Marseilles pool.

In the 1966 survey 207 live washboards were collected between river miles 0.9 and 196.1 (near Henry); however, 88.4 percent of these specimens were taken from the Alton pool between river miles 0.9 and 79.8 (Tables 8 and A-3). In the river proper no live washboard was taken between river miles 110.5 (9 miles below Havana) and 196.1. However, in 1969 a few live specimens were taken by commercial fishermen just below Peoria Lake and in Peoria Lake. At river mile 196.1 a single live washboard was collected by wading. Just above Havana at Quiver Lake two specimens were taken alive, one with the crowfoot bar and the other by wading.

In the 1896-1897 period Kelly (1899:401) examined 26 washboards collected from the river at Havana. Danglade (1914:18) found in 1912 that washboards predominated the commercial shell catch at Havana. In 1912 Forbes & Richardson (1913:533 & 536) took 11 washboards at Hennepin (river mile 207.4), and they found this species to be one of the most abundant living mussels between Henry and Chillicothe (river mile 180.4, just above the upper end of Peoria Lake). In that same year Danglade (1914:16–17) collected washboards and checked commercial shell piles containing this species from Peoria Lake. Richardson (1928:456–457) did not find a live washboard in Peoria Lake during his 1924-1925 survey. He stated that only the hardier species of mussels had been able to survive the destructive pollution period of 1917-1920 in the upper river. Evidently pollution has now virtually restricted the washboard to the lower river proper from

Table 8.—Catches of washboards (**Megalonaias gigantea**) per 5 minutes of fishing with the crowfoot bar in the Illinois River proper in the 1966 survey.

River Mile	*Number Caught Per 5 Minutes of Fishing*
0.9– 5.5	3.1
10.5– 15.1	0.3
19.2– 29.0	1.1
30.5– 39.2	0.7
40.3– 48.3	0.5
51.0– 58.9	1.2
60.8– 69.4	0.4
70.8– 79.8	0.1
80.3– 87.9	0.2
90.2–100.5	0.1
106.6–114.0	0.1
115.3–272.0[a]	0.0

[a] In this entire stretch of the river only one washboard was taken by wading at river mile 196.1. However, live specimens were taken in Bath Chute (river miles 106.8–113.3) and Quiver Lake (river miles 122.2–122.8). In 1969 live specimens were taken in the vicinity of Peoria.

below Havana to its mouth. The single specimen taken in the 1966 survey near Henry was apparently accidental. The largest estimated standing crop calculated for washboards in 1966 was 752 pounds (shell weight) per acre at river mile 51.2 (RB) in the Alton pool.

It was doubtful if a lack or scarcity of host fishes was a factor in the present limited distribution of the washboard in the river. All of the five known host fishes (Baker 1928:72) for the washboard occurred in the river in the 1960's. The gizzard shad, *Dorosoma cepedianum* (Lesueur), usually was abundant in the river from its mouth to Chillicothe, and in most years the author found that this fish occurred throughout much of the river. The white bass, *Morone chrysops* (Rafinesque), was sporadic in abundance; however, for several years the author collected this species at most of his fishing stations in the river. This host fish is known to have a tendency to migrate in the river and its bottomland lakes (Starrett & Fritz 1965:70–71) and would have been capable of disseminating the washboard throughout its original range provided the environment had been suitable for the fish and the mussel. The dogfish, *Amia calva* Linnaeus, was no longer common in the river, and the flathead catfish, *Pylodictis olivaris* (Rafinesque), was confined largely to the lower two navigation pools. As mentioned earlier, the white crappie was present in large enough numbers to have served as a host fish between the mouth of the river and Starved Rock dam.

Museum Records.—Chillicothe (1907 Freeland & Williams) USNM 677040; Peoria Narrows (1924) INHS (dead); between Peoria and Pekin (1908 F & W) USNM 677045; between Pekin and Havana (1908 F & W) USNM 678602; Quiver Lake (1955 Parmalee) ISM 1036–1037; Havana (1894 Baker) UIMNH 22173, FMNH 67963, and (1912) INHS a-22; Frederick (pre-1943 Webb Coll.) FMNH 22486; Beardstown (pre-1910) MCZ; Meredosia (1930 Morrison) USNM 678649, (pre-1910) MCZ, and (1955 Parmalee) ISM 1361–1365; Naples (1955 Parmalee) ISM 1086–1093; Pearl (1955 Parmalee) ISM 3297–3298; 1 mile N of Hardin (1956 Parmalee) ISM 2202 (dead); 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678565; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678566; 2 miles above Grafton (1907 Bartsch stat. 111) USNM 678567; Grafton (1909 Freeland) USNM 678603; and Illinois River without locality (1898) FMNH 50553.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB), 5.4–5.5 (RB), 10.5 (RB), 11.8–12.1 (LB), 14.9–15.1 (RB), 19.4 (RB), 21.7–22.0 (RB), 24.2–24.4 (LB), 27.9 (LB), 28.9–29.1 (RB), 30.5–30.8 (RB), 33.2–33.5 (RB), 39.1–39.3 (RB), 40.3–40.5 (RB), 42.2–42.3 (LB), 47.4–47.7 (LB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 53.6 (LB), 53.8 (LB), 54.3 (LB), 54.4 (RB), 56.3 (LB), 57.5–57.7 (LB), 57.6 (RB), 58.0 (RB), 58.9 (RB), 60.8 (RB), 62.6 (LB), 64.4 (LB), 66.0–66.4 (LB), 66.6 (LB), 68.6 (RB), 68.9 (RB), 69.0 (RB), 69.4

(RB), 72.9 (RB), 73.0 (RB), 79.8 (RB), 86.6 (LB), 86.8 (LB), 93.6 (LB), 96.8 (RB), 106.0–106.9 (LB), 108.8–109.0 (RB), 110.0 (RB), 110.1 (LB), 110.5 (RB), Quiver Lake, and 196.1 (LB). OSM 17705–17707 and 17709; FMNH 156700 (3), 156987 (4), 156999 (10), 157005 (4), 157008 (9), and 157009 (4). (1969): 162.3 (LB). OSM 22274.

Old Shell Records (1966 Survey).—River mile 66.0–66.4, 75.8, 86.6–86.8, 106.8, Quiver Lake, 129.8, 145.7, 156.0, 184.5, 196.1, 219.4. OSM 18219, 18253, 18270, 18290, 18301, 18312, 18329, 18359, 18382, 18431, and 18454.

Three-Ridge (Blue-Point) Amblema plicata (Say, 1817)

(Plate 1-3)

Amblema peruviana (Lamarck):
Parmalee (1967:27; 1962:9)
MCZ

Amblema costata:
Parmalee (pers. comm., 21 November 1966)
MCZ

Quadrula plicata Say:
Kelly (1899:401)
Baker (1906:78)
Forbes & Richardson (1913:529)

Unio undulatus Barnes:
Calkins (1874:45)[1]

Quadrula plicata (Say):
Danglade (1914:10)

Quadrula undulata Barnes:
Baker (1906:78)

Quadrula undulata (Barnes):
Danglade (1914:10)

Amblema rariplicata:
Richardson (1928:456)
Parmalee (pers. comm., 21 November 1966)

Amblema (Amblema) plicata plicata (Say):
FMNH

Amblema (Amblema) plicata costata Raf.:
FMNH

Amblema plicata Say, 1817 (form *rariplicata* Lam., 1819 included):
Morrison (pers. comm., 4 January 1968)

Amblema plicata:
OSM

According to Parmalee (1967:26):

> "Some authors (for example F. C. Baker, 1928) have recognized three distinct species of *Amblema: A. costata* which is associated with a headwaters or small stream environment; *A. rariplicata,* a species of medium-sized rivers, or of downstream sections of large rivers such as the Illinois and differing from the former in the shell being somewhat more elongated and inflated; and *A. peruviana,* the large river species showing an even greater degree of inflation of the shell and umbones. On the other hand, some authorities recognize only one species, and the others are considered simply as forms or variants resulting from differences in size and depth of rivers in which they occur. Again, depending upon the author consulted, the names *Crenodonta peruviana* or *Amblema plicata* are used."

A series of specimens of the genus *Amblema* collected in 1966 from the Illinois River was identified by Dr. David Stansbery as *Amblema plicata* f. *plicata* (Say, 1817). Concerning this complex Stansbery (pers. comm., 1 December 1967) stated:

> "The only type material of *Unio plicata* Say, 1817, that I could locate was at the Philadelphia Academy. . . . It is obviously a Lake Erie specimen as labeled, fits the description by Say, and has all the characteristics of *Unio peruviana* Lamarck, 1819, except size. This latter is to be expected since all the true

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[1] Baker (1928:69) lists *Unio undulatus* Barnes under *Megalonaias gigantea* (Barnes). Call's (1900: 445–446) description and Plate 13 of *U. undulatus* Barnes fit that of *Amblema plicata* (Say). Likewise, Goodrich & van der Schalie (1944:306) refer to Call's Plate 13 as *Amblema costata* Rafinesque. According to Stansbery (pers. comm., 31 July 1968): "A careful examination of Barnes' plate of the holotype of *Unio undulatus* proves it to be an eroded specimen of *Megalonaias gigantea.*" The author was of the opinion that Calkins (1874:45), like Call, was referring to *U. undulatus* as *A. plicata* rather than *M. gigantea.*

stream species found in Lake Erie are, without exception, stunted.

> "Since *Unio plicata* Say, 1817, was the first plicate naiad described from North America the name has priority. Since the smaller individuals of this complex from the Mississippi River, Ohio River, and Illinois River cannot be distinguished from these Lake Erie specimens (except for size) I conclude that *U. peruviana* Lamarck, 1819, and *U. rariplicata* Lamarck, 1819, are the *same* species and hence synonyms of *U. plicata* Say, 1817.
>
> "*All* of the forms of this complex in the Ohio River drainage & Great Lakes drainage are abundantly connected by intermediates. None is clear cut — they all 'run together.' Therefore there can be but one species. The earliest name is *U. plicata* Say, 1817, as I indicated in 1961 (1961:3, 4, & 7).
>
> "In spite of the fact that all forms in the drainage concerned are connected by intermediates there are extremes. These extremes are the compressed form *costata* Raf., 1820, found in the headwaters and the inflated form *plicata* Say, 1817, found in the big rivers (and in river-lakes such as Lake Erie). Lake Erie is in so many ways a big river with a few peculiarities of its own. Our Lake Erie *A. plicata* specimens include many form *plicata,* some form *costata,* and intermediates of every description but all somewhat stunted. No extremes of form *costata* have been taken, to my knowledge, from Lake Erie.
>
> "The compressed *costata* form of *A. plicata* is not geographically definable . . . . It is related only to habitat—to the headwaters. We do not know whether it is genetically different from the swollen *plicata* form or not. Hence, it is not definable as a subspecies. It is recognizable as a form . . . .
>
> "If we recognize forms, since *costata* Raf., 1820, is the first name given to the headwater form, *Amblema plicata* form *costata* Raf., 1820, should be used. Since the type is the swollen form, *Amblema plicata* form *plicata* (Say, 1817), should be used for it."

The author checked two specimens taken before 1918 at Havana in the collections of the Field Museum of Natural History (FMNH 68177), and these specimens were compressed much as is the form *costata.* Otherwise, all of the specimens from the river examined by the author were the swollen form *plicata.*

In 1966 the three-ridge was the most abundant mussel in the Illinois River and made up 62.4 percent of the live mussels taken in the 1966 survey (Tables 6, 7, and A-3). It was also the most important mussel taken commercially and formed 74.8 percent of the shells examined in the sorted commercial shell piles along the river (Alton pool). In the 1966 survey live mussels of all species were collected only in the three lower navigation pools, and in these pools the three-ridge accounted for the following percentages of live mussels taken: 56.9 percent in the Alton pool, 61.4 percent in the La Grange pool, and 81.2 percent in the Peoria pool. Of the 2,650 live three-ridges collected in 1966, 85.7 percent were 2.0–3.0 inches in height (Table A-12) and 87.5 percent were 7–15 years of age (Table A-13). The largest estimated standing crop of live mussels in the 1966 survey was 3,508 pounds (shell weight) per acre of three-ridges at river mile 162.3 (LB) just below the lower end of Peoria Lake.

The three-ridge was one of the more pollution-tolerant species of mussels found in the study, which probably accounts for its wide distribution and abundance in the river. In the upper sections of the La Grange pool (river miles 140.5–156.6) and Peoria pool (river miles 174.9–229.3) the three-ridge was found in small numbers but was one of the few species able to survive in those areas of the river (Table A-3). Severe pollution conditions existed in the river upstream from Peoria between 1917 and 1920, and Richardson (1928:456) mentioned that the three-ridge was the only one of the

16 species of mussels found in Peoria Lake in the 1924-1925 period that occurred in more than very scanty numbers. The aspects of pollution affecting the three-ridge and other mussels are discussed further in the next section of this paper.

In the 1966 survey subfossil three-ridge shells were taken upstream as far as river miles 253.5–256.5 in the Marseilles pool. Calkins (1874:45) collected *undulatus* from the river in La Salle County, Baker (1906:78) reported that *undulata* was taken by Handwerk at Starved Rock, and an Ohio State Museum specimen was collected there in the 1800's. In 1912 Forbes & Richardson (1913:528) took live three-ridges as far upstream as Starved Rock. Danglade (1914:13–25) found the three-ridge (blue-point and three-ridge combined) to be the most abundant mussel at the majority of his stations on the river between Henry and Grafton in 1912.

Baker (1928:74–75) reported that crappies were host fishes for the glochidia of the three-ridge. Recently in the laboratory Stein (1968:46) successfully recovered metamorphosed juveniles of *A. plicata* from infections of the yellow perch, *Perca flavescens* (Mitchill); rock bass, *Ambloplites rupestris* (Rafinesque); green sunfish, *Lepomis cyanellus* Rafinesque; bluegill, *Lepomis macrochirus* Rafinesque; and pumpkinseed, *Lepomis gibbosus* (Linnaeus). She was unable to infect several species of minnows, catfishes, and gars with glochidia of this mussel. The bluegill, green sunfish, and both species of crappies were all common fishes in the Illinois River during the 1960's.

Museum Records. — Starved Rock (pre-1900) OSM 10068; Peru (pre-1910) MCZ; Peoria (1931 Morrison) USNM 678634; between Peoria and Pekin (1908 Freeland & Williams) USNM 678594; Pekin (1907 F & W) FMNH 11206; 3 miles SE of Banner (1953 Parmalee) ISM 111 (dead); between Pekin and Havana (1908 F & W) USNM 678595; Liverpool (1957 Parmalee) ISM 2260; 2 miles N of Havana (1955 Parmalee) ISM 1008–1015; Havana (1909 Freeland) USNM 677769, (1894 Baker) UIMNH 22149, (1909) INHS, and (pre-1918 Hand Coll.) FMNH 68177; Frederick (pre-1943 Webb Coll.) FMNH 20216; 2 miles N of Beardstown (1959 Parmalee) ISM 2868; Beardstown (pre-1943 Webb Coll.) FMNH 22533 and (pre-1910) MCZ; Meredosia (1907 F & W) USNM 677036, (1930 Morrison) USNM 678635–678636, (1932 Morrison) USNM 678637, (pre-1910) MCZ, and (1955 Parmalee) ISM 1407–1412; Naples (1912 Danglade) USNM 678596 and (1955 Parmalee) ISM 1112–1117; Valley City (1909 Freeland) USNM 677766; Florence (Freeland) USNM 678592; Montezuma (shell pile) USNM 678593; Pearl (1909 F & W) USNM 677770 and (1965 Parmalee) ISM 3312; 1 mile N of Hardin (1956 Parmalee) ISM 2203 (dead); Hardin (1907 F & W) USNM 676943; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678557; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678558; 2 miles above Grafton (1907 Bartsch stat. 111) USNM 678559; and Illinois River without locality (pre-1900) OSM 23993 (dead).

Live Mussel Records (1966 Survey).— River mile 0.9–1.0 (LB), 5.4–5.5 (RB), 10.3–10.5 (RB), 11.8–12.1 (LB), 13.0 (RB), 13.2–13.5 (LB), 14.9–15.1 (RB), 19.2–19.4 (RB), 20.6–20.8 (LB), 21.7–22.0 (RB), 24.2–24.4 (LB), 25.8–26.0 (LB), 27.9 (LB), 28.9–29.1 (RB), 30.5–30.8 (RB), 33.2–33.5 (RB), 35.9–36.1 (LB), 36.1–36.3 (RB), 37.3–37.6 (RB), 39.1–39.3 (RB), 40.3–40.5 (RB), 40.5–40.7 (LB), 42.2–42.3 (LB), 42.3 (RB), 45.3–45.9 (LB), 47.4–47.7 (LB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 53.6 (LB), 53.8 (LB), 54.3 (RB), 54.4 (RB), 56.3 (LB), 56.6 (LB), 57.5–57.7 (LB), 57.6 (RB), 58.0 (RB), 58.9 (RB), 60.8 (RB), 60.8 (LB), 62.4 (RB), 62.6 (RB), 62.6 (LB), 63.8 (LB), 64.4 (LB), 64.4 (RB), 66.0–66.6 (LB), 66.9 (RB), 68.3 (RB), 68.3 (LB), 68.6 (RB), 68.9 (RB), 68.9 (LB), 69.0 (RB), 69.4 (RB), 72.0 (LB), 72.9 (RB), 73.0 (RB), 73.7 (RB), 73.7 (LB), 74.6 (RB), 75.8 (RB), 79.8 (RB), 79.8 (LB), 86.4 (LB), 86.6 (LB), 86.8 (LB), 87.3 (RB), 87.9 (LB), 93.4–93.6 (LB), 95.6 (RB), 95.8 (LB), 96.8 (RB), 98.0 (LB), 99.0–99.5 (RB), 100.0–

100.5 (LB), 106.0–106.9 (LB), 108.2–108.3 (RB), 108.8–109.0 (RB), 110.0 (RB), 110.0–110.2 (LB), 110.5 (LB), 112.1–112.5 (RB), 113.2–114.0 (LB), 115.3 (RB), 121.9–122.0 (LB), 122.2 Quiver Lake (LB), 122.8 Quiver Lake (LB), 129.8–130.4 (RB), 132.1 (RB), 135.0 (RB), 145.7 (RB), 148.5 (LB), 154.3–154.5 (RB), 155.9–156.4 (RB), 156.4–156.6 (LB), 159.4 (LB), 161.1–161.3 (LB), 161.2 (RB), 161.7–161.8 (LB), 162.3 (LB), 163.0 (LB), 164.4–165.1 (LB), 164.5–164.9 (RB), 165.2 (RB), 165.3 (LB), 166.3 (LB), 166.6 (LB), 167.2 (RB), 167.2 (LB), 167.5–167.7 (LB), 168.1–168.3 (LB), 168.1–168.5 (RB), 168.6 (LB), 169.3 (RB), 169.5 (LB), 170.8–171.8 (RB), 173.0 (RB), 174.1–174.9 (RB), 174.1 (LB), 184.5 (RB), 184.6 (RB), 184.8 (RB), 191.5 (LB), 196.1 (LB), 205.0 (RB), and 228.3 (RB). OSM 17711, 17720, 17742, 17747, 17749, 18126 (6), 18127 (5), 18128 (4), 18130 (4), 18131 (4), 18132 (3), 18133 (3), 18135 (3), 18136 (4), 18138 (4), 18139 (4), 18140 (4), 18141 (4), 18142 (4), 18143 (3), 18144 (3), 18145 (4), 18146 (2), 18147 (4), 18148 (2), 18149 (2), 18150 (2), 18151 (3), 18152 (3), 18153, 18154 (4), 18155 (4), 18156 (5), 18157 (5), and 18158; FMNH 156952 (5), 156954 (4), 156955 (3), 156958 (14), 156959 (26), 156972 (10), 156975 (3), and 156977 (7).

Old Shell Records (1966 Survey).—River mile 66.0–66.4, 75.8, 86.6–86.8, 94.3, 106.8, 145.7, 156.0, 184.5, 196.1, 196.3–198.1, 219.4, and 253.5–256.5. OSM 18218, 18252, 18269, 18278, 18291, 18328, 18358, 18430, 18442, 18453, and 18477.

Maple-Leaf

Quadrula quadrula (Rafinesque, 1820)

(Plate 1-6)

Quadrula quadrula Raf.:
  Parmalee (1967:43; 1962:9)
  Richardson (1928:457)
  Morrison (pers. comm., 4 January 1968)
  MCZ
Quadrula asperrima Lea:
  Kelly (1899:401)
  Forbes & Richardson (1913:533)
Quadrula lachrymosa Lea
  (= *quadrula* Say, *asperrimus* Lea):
  Baker (1906:79)
Quadrula lachrymosa (Lea):
  Danglade (1914:10)
Quadrula fragosa Conrad:
  Baker (1906:79)
Quadrula fragosa (Con.):
  Danglade (1914:9)
Quadrula (Quadrula) quadrula quadrula (Raf.):
  FMNH

Baker (1906:79) and Danglade (1914:9 & 10) included both *Quadrula fragosa* and *Quadrula lachrymosa* as occurring in the Illinois River. Relative to the occurrence of *fragosa* in the Illinois River Danglade (1914:40) stated:

> "Rare; an example was found in Peoria Lake, but it does not agree exactly with *fragosa* as we found it in the Cumberland River, near Clarksville, Tenn."

At a later date Baker (1928:89) wrote:

> "*Fragosa* appears rare in Wisconsin and Illinois . . . . The nearest approach in Illinois is found among specimens from Spoon River."

A large series of maple-leafs collected in the 1966 survey was studied by Dr. Stansbery, and he identified them as *Quadrula quadrula*. However, he did mention (pers. comm., 26 September 1967) that the specimens had suggestions of the *fragosa* (Conrad) description but that they were not distinguishable from his museum specimens of *Q. quadrula* from the Ohio River proper (type locale). Specimens from the Illinois River examined by the author were likewise *Q. quadrula*, including several museum specimens labeled *fragosa*. In this paper the author has treated the Illinois River *fragosa* records in the literature as being *Q. quadrula*.

In the 1966 survey the maple-leaf comprised 9.2 percent of the live mussels taken and ranked third in abundance (Tables 6 and 7). Because of its small size, this species was of little importance in satisfying the commercial demand in 1966. Of the 390 live specimens collected in the survey, 86.9 percent were 7–13 years of age (Table A-14) and 85.1 percent ranged from 1.7 to 2.5 inches in height (Table A-15).

The maple-leaf was more abundant in collections made in the Alton pool than those made in the La Grange and Peoria pools (Table A-3). In the Alton pool at river mile 72.9 (RB) a standing crop of 303 pounds per acre (shell weight) of live maple-leafs was estimated. Live specimens of this species were taken between river miles 0.9 and 210.7 (Table A-3). In the upper part of the La Grange pool (river miles 140.5–156.6), considered by the author as poor mussel habitat because of pollution, a series of eight live maple-leafs was taken. However, in the Peoria pool no live maple-leaf was collected between river mile 167.7 (lower end of Middle Peoria Lake) and mile 210.7 (between Hennepin and Spring Valley). At mile 210.7 a single live maple-leaf was taken. In the entire upper part of the Peoria pool (river miles 174.9–229.3) only 38 live mussels of all species were collected in 1966. The paucity of mussels in this part of the river was thought by the author to have been caused by pollution. As mentioned earlier, no live mussel was taken above mile 229.3. The presence of maple-leafs in the upper part of the La Grange pool indicated that this species was somewhat tolerant of pollution, but the virtual absence of the species above river mile 167.7 tended to contradict this opinion. Possibly the host fish of the maple-leaf was either scarce or absent in the upper section of the Peoria pool; however, the author was unable to ascertain the host species of this mussel (Coker 1921:23; Baker 1928:86).

At the Field Museum of Natural History the author examined a maple-leaf taken from the river at Ottawa (Starved Rock pool). Richardson (1928:456–457) stated that in 1912 the maple-leaf occurred upstream as far as Spring Valley (river mile 218.5). In 1912 Danglade (1914:40) did not consider the maple-leaf common but mentioned that it occurred in small numbers in most of the mussel beds in the river. Since Danglade's study of the river many species of mussels have disappeared or decreased in abundance. As a result of these changes, in 1966 the maple-leaf was relatively one of the most abundant species present, particularly in the Alton pool. The maple-leaf was limited in its distribution in 1966 (with the exception of the single record upstream at river mile 210.7) from Middle Peoria Lake to Grafton, whereas formerly it ranged from Ottawa to Grafton.

Museum Records.—Ottawa FMNH 22686; La Salle (pre-1910) MCZ; Peru (pre-1910) MCZ; Lake Senachwine (1934) INHS; Peoria Narrows (1924) INHS H-4; Peoria (1912 Danglade) USNM 678597; Quiver Lake (1955 Parmalee) ISM 1016–1021; Havana (1894 Baker) UIMNH 22177, (1895 Hay) FMNH 14131, and (1912) INHS a-102; 2 miles N of Beardstown (1959 Parmalee) ISM 2866–2867; Beardstown (pre-1910) MCZ; Meredosia (1930 Morrison) USNM 678638–678639, (1932 Morrison) USNM 678640, (pre-1910) MCZ, and (1955 Parmalee) ISM 1394–1400; Naples (1955 Parmalee) ISM 1140–1144; and Pearl (1965 Parmalee) ISM 3305–3307.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB), 5.4–5.5 (RB), 10.3–10.5 (RB), 13.2–13.5 (LB), 14.9–15.1 (RB), 19.2–19.4 (RB), 24.2–24.4 (LB), 25.8–26.0 (LB), 27.9 (LB), 29.0 (RB), 30.5–30.8 (RB), 33.2–33.5 (RB), 37.3–37.6 (RB), 39.1–39.3 (RB), 39.2 (LB), 40.3–40.5 (RB), 42.2–42.3 (LB), 45.3 (LB), 45.4–45.9 (LB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 53.8 (LB), 54.3–54.4 (RB), 56.3 (LB), 57.5–57.7 (LB), 57.6 (RB), 58.0 (RB), 58.9 (RB), 62.4 (RB), 62.6 (RB), 63.8 (LB), 64.4 (LB), 64.4 (RB), 66.0–66.4 (LB), 66.5 (LB), 66.6 (LB), 66.9 (RB), 68.3 (RB), 68.6 (RB), 68.9 (RB), 69.0 (RB), 72.9 (RB), 73.0 (RB), 73.7 (RB), 73.7 (LB), 74.6 (RB), 75.8 (RB), 79.8 (RB), 86.4 (LB), 86.6 (LB), 86.8 (LB), 87.9 (LB), 91.5 (RB), 93.4–93.6 (LB), 95.8 (LB), 98.0 (LB), 99.0–99.5 (RB), 100.0–100.5 (LB), 106.0–106.9 (LB), 110.0 (RB), 110.0–110.2 (LB), 110.5 (LB), 110.5 (RB), 113.2–114.0 (LB), 115.3 (RB), 118.4 (RB), 121.9–122.0 (LB), 122.2 Quiver Lake (LB), 122.8 Quiver

Lake (LB), 125.5 (RB), 129.8–130.4 (RB), 132.1 (RB), 135.0 (RB), 154.3–154.5 (RB), 155.7–156.0 (LB), 161.1–161.3 (LB), 161.7–161.8 (LB), 162.3 (LB), 166.3 (LB), 167.2 (RB), 167.2 (LB), 167.5–167.7 (LB), and 210.7 (RB). OSM 17354, 17355 (7), 17356 (11), 17357, 17358 (3), 17359, 17360, 17361 (7), 17362 (2), 17363 (4), 17364–17368, 17369, (6), 17370 (4), 17371 (3), 17372 (7), 17373 (6), 17374 (3), 17375, 17376 (3), 17377 (4), 17378 (5), 17379, 17380 (2), 17381 (4), 17382 (2), 17383 (2), 17384 (2), 17385 (11), 17386 (2), 17387 (2), 17388 (3), 17389 (16), 17390, 17391, 17392 (7), 17393 (3), 17394 (9), 17395 (5), 17396 (3), 17397 (4), 17398 (26), 17399 (21), 17400 (3), 17401 (5), 17402 (6), 17403, 17404 (8), 17405 (3), 17406 (5), 17407, 17408 (4), 17409, 17410, 17411 (4), 17412 (6), 17413 (2), 17414 (5), 17415 (19), and 17416 (7); FMNH 156950 (7), 156953 (14), 156956 (5), 156965 (5), and 156970 (10).

Old Shell Records (1966 Survey).—River mile 44.9, 66.0–66.4, 75.8, 83.0, 94.3, 106.8, Quiver Lake, 129.8, 156.0, 196.3–198.1. OSM 18195, 18264, 18280, 18292, 18302, and 18443.

Pimple-Back (Warty-Back)
Quadrula pustulosa (Lea, 1831)
(Plate 1-5)

Quadrula pustulosa (Lea):
  Parmalee (1967:40; 1962:9)
  Forbes & Richardson (1913:531)
  Danglade (1914:9)
  Coker (1921:23)
  Richardson (1928:457)
  OSM
Unio pustulosus Lea:
  Calkins (1874:44)
Quadrula pustulosa Lea:
  Kelly (1899:401)
  MCZ
Quadrula pustulosa Lea (= *dorfeuilliana* Lea, *schoolcraftensis* Lea):
  Baker (1906:79–80)
Quadrula (Pustulosa) pustulosa pustulosa (Lea):
  FMNH
Quadrula bullata Raf., 1820:
  Morrison (pers. comm., 4 January 1968)

The pimple-back was the second most abundant mussel taken in the 1966 survey (Tables 6 and 7) and it constituted 10.0 percent of all live mussels collected (Table A-3). Even though this species ranked second in abundance, its distribution was limited in 1966. In the river proper live pimple-backs were taken only between river miles 0.9 and 113.7 (about 6 miles below Havana, Table A-3). Three live specimens were collected in Quiver Lake, just above Havana. In 1969 the author obtained from a commercial mussel fisherman a live specimen of this species taken just below Peoria Lake at river mile 162.3. Most of the pimple-backs were taken in the Alton pool where they made up 14.7 percent of the catch and ranked second in abundance. The highest estimated standing crop of live pimple-backs in the Alton pool was 127 pounds per acre (shell weight) at river mile 42.3 (LB). In the La Grange pool the pimple-back ranked seventh in abundance and constituted 2.2 percent of the catch.

Coker (1921:23) mentioned that the pimple-back seldom attained a length of more than 2.5 inches. This was true for this species in the Illinois River in 1966, since only 3.5 percent of the 426 live pimple-backs taken were over 2.5 inches in length. All of these specimens were less than 2.5 inches in height (Table A-16) and 90.8 percent of them were between 6 and 12 years of age (Table A-17). The Japanese market demanded pimple-backs of 2.5 inches or more in height. The pimple-backs noted in the sorted commercial piles along the river were nearly all below the desired commercial size. Therefore, this species from the Illinois River was of little or no value for the Japanese market.

Concerning the button industry, where size was of less importance than in the pearl-culture industry, Coker (1921:23) considered the pimple-back one of the best mussels occurring in the Illinois River. Danglade (1914:40) found in 1912 that:

> "The *pustulosa*, or warty-back, is a very common shell in the Illinois, certain very productive beds yielding a large per cent of the output."

He was referring to the use of the pimple-back in the button industry.

In the 1966 survey subfossil shells of the pimple-back were taken at various locations along the river including the

Marseilles pool. Calkins (1874:44) collected this species from the river in La Salle County (Starved Rock pool). In 1912 Forbes & Richardson (1913:531) found that owing to pollution at Spring Valley (river mile 218.5) all of the mussels they collected were dead except one pimple-back. Danglade (1914:37) listed the pimple-back as occurring in the river in 1912 at all of his stations between Henry and Grafton. In the 1924-1925 period Richardson (1928:457) collected the pimple-back in Lower Peoria Lake.

Formerly the pimple-back was distributed throughout much of the river proper, but in 1966 it was limited chiefly to the lower part of the river. The present limited distribution of the pimple-back was probably the result of pollution.

According to Baker (1928:92) the channel catfish, *Ictalurus punctatus* (Rafinesque), was the known host fish for the pimple-back. The author has collected channel catfish in all five navigation pools. However, it occurred much more abundantly in the Alton and La Grange pools than in the upper three pools. Apparently the potentiality has existed for distributing young pimple-backs by the channel catfish throughout the entire La Grange pool and the lower part of the Peoria pool, but the species has been unable to reestablish itself because of unsuitable environmental conditions in this part of the river, except in the lower part of the La Grange pool and in the vicinity of Peoria.

Museum Records. — Peru (pre-1910) MCZ; Utica (Baker) FMNH 68035; Peoria (1870's) BK; between Pekin and Havana USNM 677043; Quiver Lake (1955 Parmalee) ISM 1002–1007; Havana (1894 Baker) UIMNH 22182, (1895 Hay) FMNH 14129, (1912) INHS a-107, (pre-1917 Zetek) FMNH 67964; Meredosia (1930 Morrison) USNM 678641–678642, (1932 Morrison) USNM 678643, and (1955 Parmalee) ISM 1404–1405; Naples (1955 Parmalee) ISM 1130–1135; Pearl (1965 Parmalee) ISM 3308–3309; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678560; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678561; and Illinois River without locality (pre-1900) OSM 10092.

Live Mussel Records (1966 Survey).— River mile 0.9–1.0 (LB), 10.5 (RB), 11.8–12.1 (LB), 13.0 (RB), 13.2–13.5 (LB), 14.9–15.1 (RB), 19.2–19.4 (RB), 20.6–20.8 (LB), 24.2–24.4 (LB), 29.0 (RB), 30.5–30.8 (RB), 33.2–33.5 (RB), 37.3–37.6 (RB), 39.1–39.3 (RB), 39.2 (LB), 40.3–40.5 (RB), 42.2–42.3 (LB), 45.3 (RB), 45.3 (LB), 45.4–45.9 (LB), 47.4–47.7 (LB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 53.6 (LB), 53.8 (LB), 54.3 (RB), 54.4 (RB), 56.3 (LB), 57.5–57.7 (LB), 58.0 (RB), 58.9 (RB), 60.8 (RB), 62.4 (RB), 62.6 (RB), 62.6 (LB), 63.8 (LB), 64.4 (LB), 66.0–66.6 (LB), 66.9 (RB), 68.3 (RB), 68.6 (RB), 68.9 (LB), 69.0 (RB), 72.9 (RB), 73.0 (RB), 74.6 (RB), 75.8 (RB), 79.8 (RB), 79.8 (LB), 98.0 (LB), 106.0–106.9 (LB), 110.0 (RB), 113.7 (LB), and Quiver Lake. OSM 17345, 18129 (2), 18134, 18137 (3); FMNH 156970 (2), 156982 (7), 156983 (5), 157002 (13), and 157004 (5). (1969): 162.3 (LB). OSM 22276.

Old Shell Records (1966 Survey).— River mile 44.9, Meredosia Lake, 66.0–66.4, 75.8, 94.3, 106.8, Quiver Lake, 129.8, 145.7, 156.0, 196.1, 196.3–198.1, 219.4, and 253.5–256.5. OSM 18196, 18254, 18262, 18281, 18293, 18303, 18313, 18330, 18360, 18432, 18444, 18455, and 18478.

Warty-Back

Quadrula nodulata (Rafinesque, 1820)

(Plate 2-7)

Quadrula nodulata (Raf.):
    Parmalee (1967:39; 1962:9)
Quadrula nodulata Raf., 1820:
    Morrison (pers. comm., 4 January 1968)
Unio pustulatus Lea:
    Calkins (1874:44)
Quadrula pustulata Lea:
    Kelly (1899:401)
    Baker (1906:80)
Quadrula pustulata (Lea):
    Danglade (1914:9)
Quadrula (Pustulosa) nodulata (Raf.):
    FMNH

The warty-back ranked seventh in abundance (Tables 6 and 7) and accounted for 1.6 percent of the live mussels taken in the 1966 survey (Table A-3). Sixty-eight live warty-backs were collected between river miles 0.9 and

95.8 (below Browning). However, 92.6 percent of these specimens were taken in the Alton pool, and in that pool the species ranked fifth in abundance. The warty-backs collected in the survey ranged from 5 to 14 years in age (Table A-18). No specimen of this species taken in the 1966 Illinois River collections exceeded 2.0 inches in height, and the warty-back was therefore too small to have any value for the pearl-culture industry. According to Danglade (1914: 39), in 1912 the warty-back was usually classed with the pimple-back (*Q. pustulosa*) but was of lesser quality for use in the button industry.

Calkins (1874:44) reported collecting this species from the river in La Salle County (Starved Rock pool). Forbes & Richardson (1913) did not collect the warty-back in their 1912 survey between Morris and Chillicothe. However, in 1966 a subfossil shell of this species was taken from that section of the river at river mile 196.1 (Henry). Danglade (1914:39) stated that the warty-back was distributed generally throughout the river but occurred in very small numbers. However, in his 1912 survey (Danglade 1914:37) he did not record taking this species any farther upstream than Havana. In the period of 1896-1897, Kelly (1899:401) examined 20 warty-backs collected at Havana. The museum records of this species listed below were limited to specimens from the lower river. Likewise, the subfossil shells of the warty-back taken in 1966 were all confined to the lower river except for the one record at river mile 196.1. Apparently this species was not common in the Illinois River above Havana even before 1913, and it seems to have been eliminated from the middle and upper river by pollution before 1920.

Possible fish hosts for the warty-back listed by Baker (1928:96) were the white crappie; black crappie; largemouth bass, *Micropterus salmoides* (Lacépède); and bluegill. All of these fish species occurred in the river.

Museum Records.—Havana (pre-1900 Strode) FMNH 50478, (1894 Baker) UIMNH 22178, and (1895 Hay) FMNH 14130; Meredosia (1930 Morrison) USNM 678644–678645, (1932 Morrison) USNM 678646, and (1955 Parmalee) ISM 1401–1403; Naples (1955 Parmalee) ISM 1136–1139; Pearl (1965 Parmalee) ISM 3304; and 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678562.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB), 11.8–12.1 (LB), 13.0 (RB), 21.7–22.0 (RB), 33.2–33.5 (RB), 37.3–37.6 (RB), 39.1–39.3 (RB), 40.5–40.7 (LB), 42.3 (LB), 45.3 (RB), 45.3 (LB), 45.4–45.9 (LB), 47.4–47.7 (LB), 54.3 (RB), 62.4 (RB), 64.4 (LB), 66.0–66.4 (LB), 66.5 (LB), 66.9 (RB), 73.0 (RB), 73.7 (LB), 74.6 (RB), 75.8 (RB), 86.6–86.8 (RB), 86.8 (LB), 95.8 (LB). OSM 17338, 17339 (2), 17340 (3), 17341, 17346 (14), 17348 (9), 17349, 17350, 17351 (3), 17352, and 17353; FMNH 156947 (4), 156948, and 156992 (2).

Old Shell Records (1966 Survey).—River mile 44.9, 75.8, 83.0, 86.6–86.8, and 196.1. OSM 18197, 18265, 18271, and 18433.

Monkey-Face

Quadrula metanevra (Rafinesque, 1820)

Quadrula metanevra (Raf.):
    Parmalee (1967:39; 1962:9)
    Danglade (1914:10)
Unio metanevrus Raf.:
    Calkins (1874:43)
Quadrula metanevra Raf.:
    Kelly (1899:401)
    Baker (1906:79)
    MCZ
Quadrula metanevra wardii Lea:
    Baker (1906:79)
Quadrula (Orthonymus) metanevra (Raf.):
    FMNH

Danglade (1914:40) considered the monkey-face a rare species in the Illinois River. In his 1912 survey (1914:37) he took a few specimens at Peoria Lake, Bath, the old La Grange locks, Meredosia, Bedford, Pearl, and Grafton (possibly the Mississippi River). In 1874 Calkins (1874:43) reported that the monkey-face occurred abundantly in the upper river (Starved Rock pool). In the early 1930's Morrison (pers. comm., 27 November 1967) did not collect a live specimen of this species at Meredosia. Likewise, Parmalee (pers. comm., 21 November 1966) did not take a live monkey-face in his collections in the lower river in the 1950's. However, he did collect subfossil shells of this species at Naples and Meredosia. No live specimen of this species was taken in our 1966 survey, but a few subfossil shells were found between river miles 94.3 and 219.4.

Baker (1928:99) stated that:

> "*Metanevra* is a species of both large and small rivers where it lives in the channel on a gravel bottom in deep water, where there is a good current . . . . Rare on a mud bottom."

The scarcity of the monkey-face in the middle and lower parts of the river, even before 1913, probably was related to the scarcity of gravel bottoms in that section of the river. The upper river, before dams were constructed and pollution became severe, may have provided a more suitable environment for this species than the middle and lower river.

The bluegill and the sauger, *Stizostedion canadense* (Smith), were reported by Baker (1928:99) as the host fishes for the monkey-face. The bluegill was a common fish in the lower three pools of the river, but the sauger was uncommon.

Museum Records. — Starved Rock (pre-1904 Conrad) FMNH 68124; La Salle (pre-1910) MCZ; and Havana INHS.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 94.3, 145.7, 156.0, and 219.4. OSM 18279, 18331, 18361, and 18456.

Buckhorn (Pistol-Grip)

Tritogonia verrucosa (Rafinesque, 1820)

Tritogonia verrucosa (Barnes):
 Parmalee (1967:43; 1962:9)
Unio tuberculatus Barnes:
 Calkins (1874:45)
Tritogonia tuberculata Barnes:
 Baker (1906:70)
 Forbes & Richardson (1913:531)
 Richardson (1928:458)
 MCZ
Tritogonia tuberculata (Barnes):
 Danglade (1914:10)
Tritogonia verrucosa Raf., 1820:
 Morrison (pers. comm., 4 January 1968)
 MCZ
Tritogonia verrucosa verrucosa (Raf.):
 FMNH

In 1912 Danglade (1914:43) considered the buckhorn widely distributed but comparatively rare in the Illinois River. Calkins (1874:45) found in the early 1870's that this species occurred abundantly in the upper river (Starved Rock pool). Danglade (1914:37) reported taking the buckhorn at most of his stations on the river between Henry and Grafton. In 1912 Forbes & Richardson (1913:531–537) did not take the buckhorn in their collections at Hennepin but did collect it in the Illinois River opposite Lake Depue and in the river between Henry and Chillicothe. This species was not taken in Peoria Lake in the 1924-1925 period by Richardson (1928:457–458). In 1930 Morrison (pers. comm., 4 January 1968) collected live buckhorns from the river at Meredosia. Twenty-five years later Parmalee (pers. comm., 21 November 1966) also took live specimens of this species at Meredosia; however, he did not take a live buckhorn at any of his other collecting stations in the river in the 1950's. No live specimen of this species was collected from the river in the 1966 survey; however, two buckhorns were taken alive in 1969 by a commercial mussel fisherman from the river at Peoria just below Peoria Lake. This species possibly still occurs in the Alton pool, as indicated by Parmalee's 1955 record at Meredosia.

Apparently the buckhorn had disappeared from the river above Peoria before 1924 (Richardson 1928:457–458) as a result of pollution and is now rare in the lower part of the Peoria pool and possibly in the Alton pool. The museum and old shell records and literature citations presented here indicated that the buckhorn formerly occurred in all of the navigation pools of the river.

The host fish of the buckhorn is not known.

Museum Records.—Peru (pre-1910) MCZ; Peoria (1870's) BK and (1878) INHS; between Pekin and Havana (1907 Freeland & Williams) USNM 678598; Havana (1894 Baker) UIMNH 22176, (1895 Hay) FMNH 8342, and (1910 Zetek) FMNH 59188 and 68172; Grand Point (possibly Grand Island near Bath) (Freeland) USNM 678599;

Meredosia (pre-1910) MCZ, (1930 Morrison) USNM 678647–678648, and (1955 Parmalee) ISM 1419–1420; and Naples (1955 Parmalee) ISM 1094–1095 (dead).

Live Mussel Records (1966 Survey).—None. (1969): River mile 162.3 (LB). OSM 22275.

Old Shell Records (1966 Survey).—River mile 44.9, 106.8, 145.7, 156.0, 219.4, and 253.5–256.5. OSM 18198, 18294, 18332, 18362, 18457, and 18480.

Purple Warty-Back
Cyclonaias tuberculata (Rafinesque, 1820)

Cyclonaias tuberculata Raf.:
  Parmalee (1967:27; 1962:9)
Unio verrucosus Barnes:
  Calkins (1874:46)
Quadrula tuberculata Bar.:
  Kelly (1899:401)
Quadrula granifera Lea:
  Kelly (1899:401)
  Baker (1906:82)
Quadrula tuberculata Raf. (= *verrucosa* Barnes):
  Baker (1906:81–82)
Quadrula granifera (Lea):
  Danglade (1914:9)
Quadrula tuberculata (Raf.):
  Danglade (1914:9)
Cyclonaias tuberculata granifera (Lea):
  Baker (1928:107)
Rotundaria tuberculata Raf., 1820:
  Morrison (pers. comm., 4 January 1968)

Danglade (1914:38) listed two species of purple warty-backs (*Q. granifera* and *Q. tuberculata*) as occurring in the Illinois River in 1912. Regarding *granifera* he stated (Ibid.) that:

> "This is a rather rare shell in the Illinois, although a few examples were found in the upper half of the shell-producing portion of the river at Chillicothe, Peoria, Havana, and Bath. It is an inflated shell, heavy anteriorly, and reaches a good size, but on account of its dull purple nacre it is not now used for the manufacture of buttons."

Danglade (1914:38) considered *tuberculata* as rare in the river and commented that:

> "some examples of this mussel were found in the lower stretches of the river where the water is swifter, as below the Government locks at La Grange, at Diamond Island, and at Hardin. There appears to be a more or less gradual change from the inflated *granifera* of the upper stretches, where there is but little current and the bottom is composed largely of soft mud, to the much flatter *tuberculata* of the lower river where the bottom is harder and the current is stronger."

Baker (1928:103–109) recognized three ecological forms of *Cyclonaias tuberculata*: (i) *compressa,* a flat shell found in small streams; (ii) *tuberculata,* a wider and more elongated shell than *compressa* occurring in medium-sized rivers like the upper Ohio and the Illinois; and (iii) *granifera,* which was smaller and wider and had higher umbones and a more corpulent shell than *tuberculata* and which inhabited the large rivers, such as the Mississippi and the lower Illinois. Even though Baker (1928:109) mentioned that the form *granifera* occurred in the lower Illinois River, he (1928:108) stated that he had not seen this form from the river. Concerning this species in Indiana, Goodrich & van der Schalie (1944:306) stated that:

> "In passing from the mid-portion of a large stream such as the Wabash into the region at and below Terre Haute one finds that this species has coarser pustules. Formerly the name *granifera* was applied to the large-river phase of *C. tuberculata.* It is now known that *granifera* is merely an ecological form."

This species was not taken alive in the 1966 survey of the Illinois River. Neither Morrison (pers. comm., 4 January 1968) in the 1930's nor Parmalee (pers. comm., 21 November 1966) in the 1950's took a live specimen of this species in their collections from the river. Parmalee (Ibid.) did find several old shells of this species at Naples in 1955. In the period of 1896-1897, Kelly (1899:401) examined 18 specimens of *Q. tuberculata* and a specimen of *Q. granifera* collected near Havana. Calkins

(1874:46) reported that the purple warty-back occurred in the upper river (Starved Rock pool). This species was not taken in the upper and middle river collections made in 1912 by Forbes & Richardson (1913).

A specimen collected from the river at Havana in 1912 (INHS A-224) was identified by Stansbery (pers. comm., 20 July 1967) as the *granifera* (Lea, 1838) form of *C. tuberculata*. The few subfossil shells of this species taken in the 1966 survey between river miles 94.3 and 256.5 appeared to be less inflated than the aforementioned form *granifera* specimen. Morrison (pers. comm., 4 January 1968) referred to the U.S. National Museum specimens listed below from the river as *Rotundaria tuberculata* and made no mention of form. Likewise, Parmalee (pers. comm., 21 November 1966) listed the above mentioned dead shells he collected at Naples as *Cyclonaias tuberculata*.

Because of the limited number of specimens examined during this study, the author agrees with Stansbery (pers. comm., 31 July 1968) that the purple warty-back should be referred to simply as *Cyclonaias tuberculata*.

The host fish for the purple warty-back is not known.

Museum Records. — Near Chicago (Calkins) USNM 25998; Chillicothe (1907 Freeland & Williams) USNM 676963 and 677041; and Havana (1912) INHS A-224.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— River mile 94.3, 219.4, 240.4, and 253.5–256.5. OSM 18283, 18458, 18467, and 18479.

Bullhead (Sheepnose)

Plethobasus cyphyus (Rafinesque, 1820)

Plethobasus cyphyus (Raf.):
Parmalee (1967:35; 1962:9)
Unio Aesopus Green:
Calkins (1874:41)
Pleurobema aesopus Green:
Baker (1906:77)
Pleurobema aesopus (Green):
Danglade (1914:10)

In the early 1870's Calkins (1874:41) found this species occurring abundantly in the Illinois River in La Salle County (Starved Rock pool). Baker (1906:77) reported that the bullhead mussel was collected at Havana. This species was not reported from the upper river in 1912 by Forbes & Richardson (1913). Danglade (1914:41) considered this species rare in the Illinois River in 1912, and he collected live specimens only at Bath and Meredosia. Regarding the bullhead, he stated: "It is brittle and not a good button shell; moreover, being so uncommon in the Illinois, it is disregarded altogether."

No live specimen of this species was taken in the 1966 survey. One subfossil shell was collected at river mile 94.3 (near Browning). Parmalee (pers. comm., 21 November 1966) found dead shells of this species in 1955 at Naples, but he took no live specimen of this species in his collections during the 1950's. Likewise, Morrison (pers. comm., 27 November 1967) did not take a live bullhead mussel in his river collections in the early 1930's.

Regarding the present status of this species in Illinois, Parmalee (1967:35) considered it to be restricted to the Mississippi and Wabash rivers where it was generally uncommon to rare.

Evidently by 1912 the bullhead was a rare species existing only in the lower part of the river. The museum records indicated that the species once occurred upstream as far as Morris (Marseilles pool). Because of these records and other evidence presented here, it appeared to the author that the bullhead formerly occurred throughout much of the river in limited numbers and in the upper river abundantly (Calkins 1874: 41). Evidently pollution and the reduction in current caused by the dams eliminated this species from the river.

The host fish for this species was believed by Baker (1928:112) to have been the sauger.

Museum Records. — Near Chicago ("one very old example, perhaps 50 years old when collected" Calkins) USNM 84315; Morris (Shimek Coll.) USNM 515034; and Illinois River without locality (1870's) BK and ("including one example 40 years old" John Wolf, ex James Lewis) USNM 25987.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 94.3. OSM 18282.

Pleurobema cordatum Complex

Pleurobema cordatum (Raf.):
  Parmalee (1967:35)
  van der Schalie (pers. comm., 31 August 1967)
Unio coccineus Lea:
  Calkins (1874:42)
Unis[*o*] *solidus* Lea:
  Calkins (1874:45)
Unio obliquus Lam.:
  Calkins (1874:44)
Quadrula obliqua Lamarck:
  Baker (1906:80–81)
Quadrula coccinea Conrad (= *catillus* Conrad):
  Baker (1906:81)
Quadrula solida Lea (= *fulgidus* Lea):
  Baker (1906:81)
Quadrula pyramidata Lea:
  Baker (1906:81)
Quadrula pyramidata (Lea):
  Danglade (1914:9)
Quadrula plena (Lea):
  Danglade (1914:9)
Quadrula solida (Lea):
  Danglade (1914:9)
Quadrula coccinea (Con.):
  Danglade (1914:9)
Quadrula obliqua (Lam.):
  Danglade (1914:9)
Quadrula obliqua (Lamarck):
  Coker (1921:25)
Pleurobema plenum:
  Richardson (1928:458)
Pleurobema catillus var. *solida*:
  Richardson (1928:458)
Pleurobema catillus var. *coccinea*:
  Richardson (1928:458)
Pleurobema cordatum:
  Richardson (1928:458)
Pleurobema coccineum solida (Lea):
  Baker (1928:118)
Quadrula (Obliquata) catillus (Conrad):
  FMNH
Quadrula (Obliquata) coccinea coccinea (Conrad):
  FMNH
Quadrula (Obliquata) obliquata (Raf.):
  FMNH
Pleurobema (cordatum) pyramidatum:
  Parmalee (1962:9)
Pleurobema c. coccineum:
  Parmalee (1962:9)

Danglade (1914:9 & 39) recognized five species of mussels of this complex occurring in the Illinois River in 1912, all of which he considered rare except *Q. obliqua*. About this species Danglade (1914:39) stated:

> "This shell, while not a common one in the Illinois, is found generally distributed throughout the river. It furnishes good button material, but is hardly equal in size or quality to the species in the Ohio River beds."

He (1914:37) did not record taking any species of this complex from the river above Peoria Lake.

No live specimen belonging to this complex was taken in the 1966 survey of the Illinois River. Likewise, neither Parmalee (pers. comm., 21 November 1966) in the 1950's nor Morrison (pers. comm., 27 November 1967) in the 1930's collected any living specimens of this complex from the river.

Calkins (1874:42, 44, & 45) reported that *U. coccineus* occurred abundantly in the Illinois River in La Salle County (Starved Rock pool). He also found *U. obliquus* in the river in association with *U. solidus*. Baker (1906:80–81) reported four species of this complex from the Illinois River. Coker (1921:25) stated that *Q. obliqua* was found in the Illinois River. However, Baker (1928:137) did not find this species in the Hinkley and Daniels collections from the Illinois River. *Pleurobema coccineum solida* was reported by Baker (1928:120) as occurring in the Illinois.

Van der Schalie (pers. comm., 31 August 1967) informed the author of two old records of *Pleurobema cordatum* (forma?) from the Illinois River in the collections of the University of Michigan Museum of Zoology. He wrote:

> "This species was studied by Ortmann and he clearly indicated that the forms all belong to the central *P. cordatum* complex. It would simplify matters if the name *Pleurobema cordatum* were used and then append the form names *coccineum* (small river form) and *catil-*

COLOR PLATES

Live Mussels

Collected in the 1966 Survey

of the Illinois River

PLATE I

1. Floater, **Anodonta grandis grandis** Say
2. Floater, **Anodonta grandis corpulenta** Cooper
3. Three-Ridge, **Amblema plicata** (Say)
4. Washboard, **Megalonaias gigantea** (Barnes)
5. Pimple-Back, **Quadrula pustulosa** (Lea)
6. Maple-Leaf, **Quadrula quadrula** (Raf.)

PLATE 2

7. Warty-Back, **Quadrula nodulata** (Raf.)
8. Paper Pond Shell, **Anodonta imbecillis** Say
9. Fragile Heel-Splitter, **Proptera laevissima** (Lea)
10. Pink Heel-Splitter, **Proptera alata** (Say)
11. Fragile Paper Shell, **Leptodea fragilis** (Raf.)
12. White Heel-Splitter, **Lasmigona complanata** (Barnes)

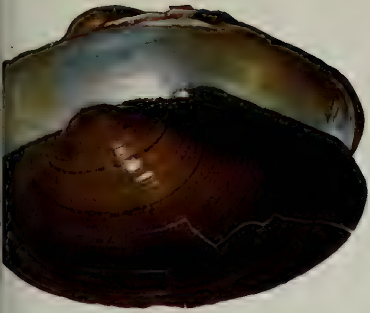
PLATE 3

13. Rock Pocketbook, **Arcidens confragosus** (Say)
14. Pig-Toe, **Fusconaia flava** forma **undata** (Barnes)
15. Three-Horned Warty-Back, **Obliquaria reflexa** Raf.
16. Slough Sand-Shell, **Lampsilis anodontoides** forma **fallaciosa** (Smith)
17. Fat Mucket, **Lampsilis radiata luteola** (Lamarck)
18. Ebony Shell, **Fusconaia ebena** (Lea)

PLATE 4

19. Heel-Splitter, **Anodonta suborbiculata** Say
20. Hickory-Nut, **Obovaria olivaria** (Raf.)
21. Deer-Toe, **Truncilla truncata** Raf.
22. Fawn's Foot, **Truncilla donaciformis** (Lea)
23. Liliput Shell, **Carunculina parva** (Barnes)

The color plates were printed before live specimens of the Buckhorn, **Tritogonia verrucosa** (Raf.), were collected from the Illinois River in 1969.



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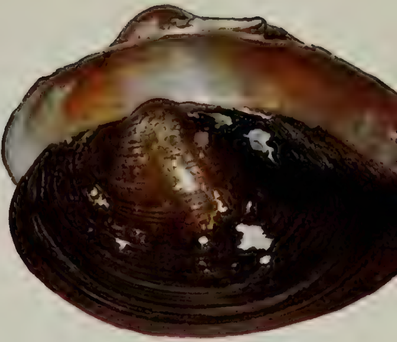

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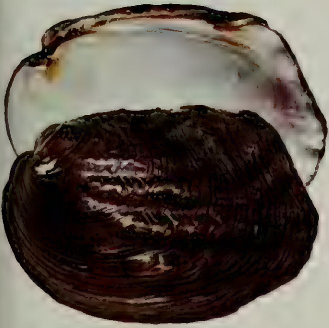

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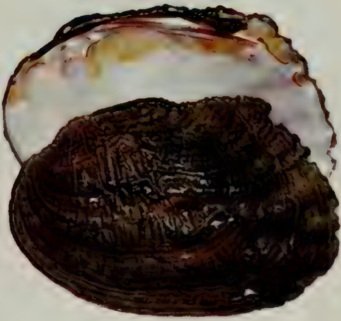

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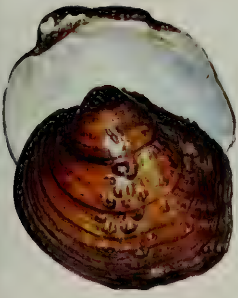

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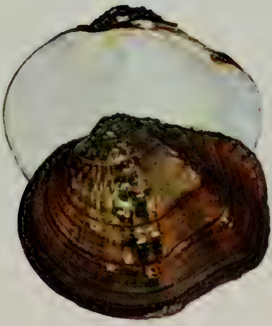

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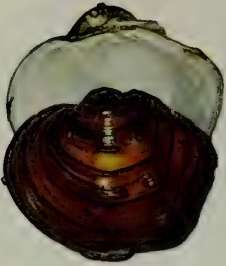
PLATE 1 — Illinois River Mussels



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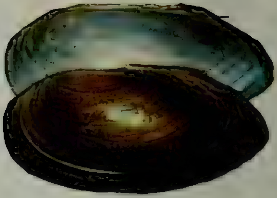

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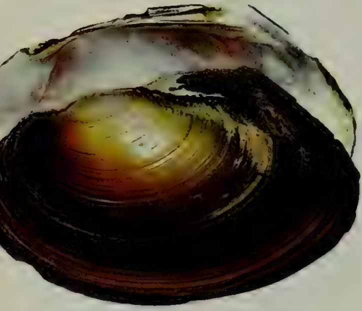

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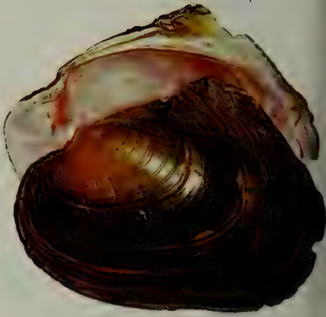

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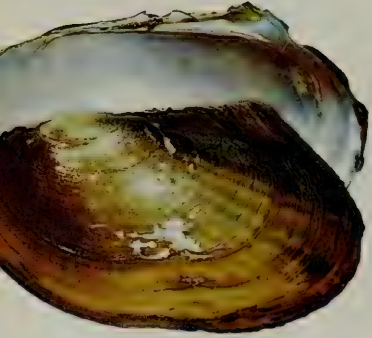

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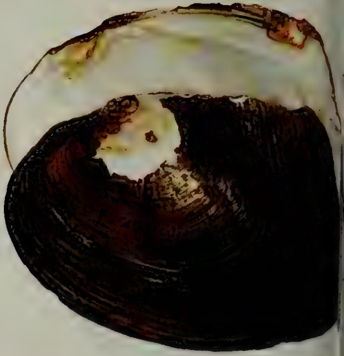

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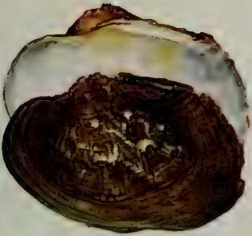
PLATE 2 — Illinois River Mussels



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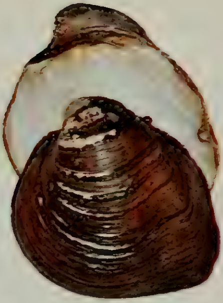

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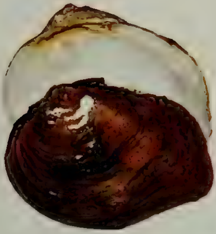

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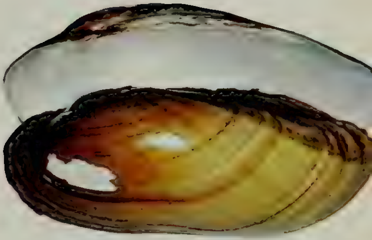

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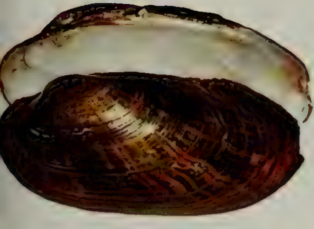

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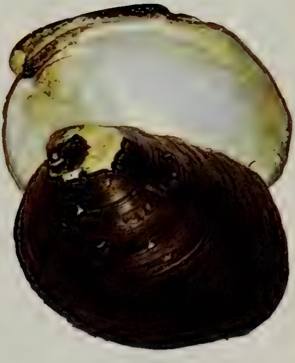

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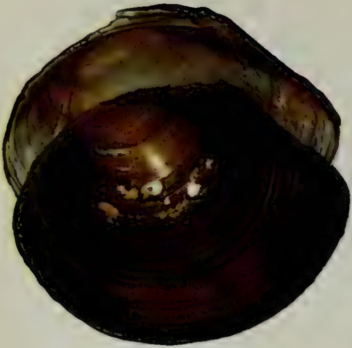
PLATE 3 — Illinois River Mussels



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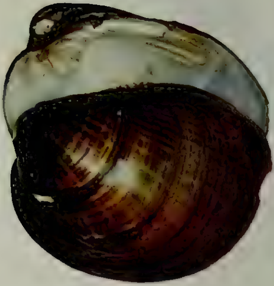

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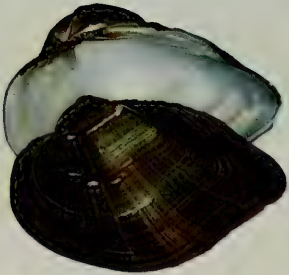

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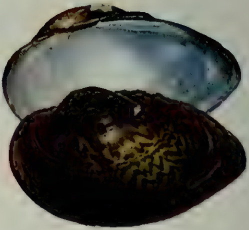

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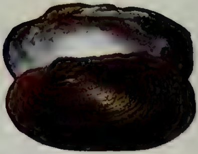

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PLATE 4 — Illinois River Mussels

> *lus* or *pyramidatum* which really are the forms that occur in a large river like the Illinois. Most certainly there is no such species (following Ortmann) as *Pleurobema pyramidatum* that should be listed as a separate entity."

Relative to the *P. cordatum* complex in the Illinois River, Parmalee (pers. comm., 29 June 1967) stated:

> "I encountered dead shells (and have some in the collections) commonly at Naples, 2 miles north of Meredosia and 3 miles S.E. of Banner. This was undoubtedly a common species in the Illinois River before pollution and silting. In my opinion and interpretation, *cordatum* is the species and *coccineum, catillus* and *pyramidatum* are all subspecies or variants."

The author examined several specimens belonging to this complex from the river at the Field Museum of Natural History. These specimens were catalogued as to subspecies, and their respective museum numbers were listed later under *Pleurobema cordatum* complex. After conversing with Dr. David H. Stansbery about this complex, the author had no confidence in his own identifications of these museum specimens.

Because of differences of opinion that existed among taxonomists concerning the nature of the *P. cordatum* complex, the author decided to use here only the scientific names applied to old shells of this complex collected in the 1966 surveys and to shell specimens from the river he submitted to Dr. Stansbery for identification. These specimens were deposited in The Ohio State Museum. Stansbery (1967) recently has done extensive work with this complex and has revised it into three described and one undescribed species. Stansbery (pers. comm., 31 July 1968) noted that he could not with clear conscience lump all the species of the *P. cordatum* complex under a single name, since he could demonstrate neither the existence of a cline nor the existence of intermediates connecting these species. This was in essential agreement with Baker (1928: 113–123). As a result of Dr. Stansbery's identifications, the author has accepted two species of this complex as once having occurred in the Illinois River: (i) *Pleurobema coccineum* forma *solida* (Lea, 1838) and (ii) *Pleurobema pyramidatum* (Lea, 1831). Museum specimens not checked by Dr. Stansbery have been listed below under *P. cordatum* complex.

Pleurobema coccineum forma **solida** (Lea, 1838)

Museum Records. — Havana (1894) OSM 19232; Meredosia (1913) OSM 19231; and Illinois River without locality (1870's) OSM 5018.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— River mile 44.9, 66.0, 196.3–198.1, and 219.4. OSM 18200, 18220, 18445, and 18459.

Pleurobema pyramidatum (Lea, 1831)

Museum Records.—Illinois River without locality (pre-1900) OSM 19230.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— None.

Pleurobema cordatum Complex

Museum Records. — Starved Rock (Frierson Coll.) UMMZ 79705; Canton [?] (pre-1943 Webb Coll.) FMNH 22694; 3 miles SE of Banner (1953 Parmalee) ISM 819 (dead); Havana (1895 Hay) FMNH 6439; and Illinois River without locality FMNH 14313 and (James Lewis) UMMZ 79667.

Elephant's Ear
Elliptio crassidens (Lamarck, 1819)

Elliptio crassidens (Lamarck):
  Parmalee (1967:29; 1962:9)
  Richardson (1928:458)
Unio crassidens Lam.:
  Calkins (1874:42)
Unio crassidens Lea:
  Baker (1906:77)
Unio crassidens (Lea):
  Danglade (1914:10)

Parmalee (1962:9) listed 11 specimens of this species from the Kingston Lake Site middens (1100–1400 AD) located adjacent to the Illinois River 15 miles southwest of Peoria. It was presumed that these specimens had been taken by the Indians from the river. Calkins (1874:42) considered the elephant's ear an abundant species in the Illinois River in La Salle County (Starved Rock pool). This species was reported from the river at Utica by Baker (1906:77). Danglade (1914:37) collected this mussel from the Illinois River in 1912 at Chillicothe, Bath, Meredosia, Florence, Pearl, Kampsville, Diamond Island, Hardin, Twelve-Mile Island, and Grafton (possibly Mississippi River). Relative to the elephant's ear in the Illinois, Danglade (1914:41) noted:

> "Rare; although found in most of the beds, the percentage is so small that it is practically a negligible quantity. The nacre varies from pink to white. This shell is used for making novelties."

The elephant's ear was not collected from the upper river in 1912 by Forbes & Richardson (1913).

In the 1966 survey only two old shells of this species were collected and no live specimen was taken. Parmalee (pers. comm., 21 November 1966) collected dead shells of this species in 1955 at Naples. The elephant's ear was not taken from the river by Morrison (pers. comm., 27 November 1967) in the early 1930's.

Formerly this species occurred in much of the Illinois River; however, except in the upper river it apparently was never abundant. It probably disappeared from the river before 1930.

The host fish for the elephant's ear is not known.

Museum Records. — Havana (1894 Baker) UIMNH 22172; and Meredosia (1913) INHS.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— River mile 129.8 and 156.0. OSM 18314 and 18363.

Lady-Finger (Spike)
Elliptio dilatatus (Rafinesque, 1820)

Elliptio dilatatus (Raf.):
- Parmalee (1967:29; 1962:9)
- Richardson (1928:457)
- MCZ

Unio gibbosus Barnes:
- Calkins (1874:42)
- Kelly (1899:401)
- Forbes & Richardson (1913:536)

Unio gibbosus Barnes (= *arctior* Lea):
- Baker (1906:76–77)

Unio gibbosus (Barnes):
- Danglade (1914:10)

Elliptio (Eurynia) dilatatus dilatatus (Raf.):
- FMNH

Elliptio dilatatus Raf., 1820:
- Morrison (pers. comm., 4 January 1968)

Calkins (1874:42) collected this species from the river in La Salle County (Starved Rock pool) in the early 1870's. In the period of 1896-1897, Kelly (1899:401) examined 25 specimens of lady-fingers collected in the Havana area. In 1912 Forbes & Richardson (1913:535 & 536) did not collect this species any farther upstream than Henry. Danglade (1914:37) reported taking this mussel in 1912 at all of his principal collecting stations in the river between Henry and Grafton. However, by 1925 Richardson (1928:454–457) found that pollution had destroyed this species in the upper river above Lower Peoria Lake.

Concerning this species in the Illinois River Danglade (1914:41–42) wrote:

> "The lady-finger is not now a commercial shell unless it be white, which is seldom the case. It is found in large quantities along the river, some beds, which the clammers avoid as much as possible, having a very large percentage. Above the upper bridge at Peoria there are two small beds of this species; one bed consists mostly of white nacred shells, while in the other the nacre is the ordinary dull purple color. At Meredosia a driveway leading from the river to the bank above is covered with about 60 tons of these shells. They had been purchased at a low price in the hope that there would be a demand for them. Button cutters claim that even the white *gibbosus* do not make good blanks on account of the shell being brittle."

Morrison (pers. comm., 27 November 1967) did not collect this species at Meredosia in 1930, whereas 20 years earlier it apparently was abundant in that area, as indicated by Danglade. In 1955 Parmalee (pers. comm., 21 November 1966) collected only dead shells of this species at Naples, Meredosia, and near Banner. No live specimen of this species was taken in the 1966 survey, but dead shells were collected at various points along the river.

The lady-finger formerly was an abundant mussel found throughout most of the river. The species probably was eliminated by pollution and siltation between 1925 and 1955.

The fish host of the lady-finger is not known.

Museum Records.—Spring Bay Narrows (1912 Danglade) USNM 678600; Peoria Narrows (1924) INHS 1-F; Peoria Lake (pre-1910) MCZ; Peoria (1870's) BK; Havana (1894 Baker) UIMNH 22174 and (1912) INHS A-33; Grand Island (1912 Danglade) USNM 678601; Naples (1955 Parmalee) ISM 1156–1157 (dead); 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678563 and (1907 Bartsch stat. 109) USNM 678564; and Illinois River without locality (pre-1943 Webb Coll.) FMNH 22017 and (pre-1910) MCZ.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 44.9, 66.0–66.4, 75.8, 94.3, 106.8, 129.8, 145.7, 156.0, 167.2, 184.5, 219.4, and 253.5–256.5. OSM 18199, 18221, 18255, 18284, 18295, 18315, 18333, 18364, 18378, 18384, 18460, and 18481.

Pond-Horn

Uniomerus tetralasmus (Say, 1830)

Uniomerus tetralasmus (Say):
Parmalee (1967:44)
Unio tetralasmus Say (= *jamesianus* Lea):
Baker (1906:77)

In the collection of the University of Illinois Museum of Natural History the author examined a specimen of this species collected at Havana by Baker in 1894. However, the label did not specify Illinois River. Baker (1906:77) did not mention this record from Havana but did state that this species had been collected from Phelps Lake, Fulton County. Relative to Phelps Lake, Kofoid (1903:414–415) noted:

> "This body of water lies on the western side of the river about a mile below the city of Havana, in the elevated bottom-lands below the mouth of Spoon River. . . . At river stages of 11 ft. and above, backwater from Spoon River makes its way through a now abandoned channel to the lake and thence out to the river through the slough."

The river Kofoid referred to was the Illinois River. Phelps Lake was drained and leveed off for agricultural purposes about 60 years ago. The author is of the opinion that the UIMNH specimen labeled Havana was the record referred to by Baker as from Phelps Lake.

No other record or specimen of this species from the river and its adjoining bottomland lakes was located by the author.

Museum Records. — Havana (1894 Baker) UIMNH 22147.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Lastena lata (Rafinesque, 1820)

Lastena lata (Rafinesque):
Parmalee (1967:87)
Lastena lata Rafinesque (= *dehiscens* Say):
Baker (1906:73)

Baker (1906:73) reported that Marsh collected this species from the Illinois River. This is the only report known to the author of this species having been found in this river. Goodrich & van der Schalie (1944:308) considered this a rare shell throughout its range. According to Stansbery (pers. comm., 31 July 1968):

> "A review of the literature and museum collections reveals this species as restricted to the Ohio River drainage system. It would not be expected from the Illinois River. It is apparently absent from all of its range except the Green River of the Kentucky and the Clinch River of the Southern Appalachians."

In the author's opinion the record by Baker should be considered doubtful.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Subfamily ANODONTINAE
(Rafinesque, 1820) Ortmann, 1910

Rock Pocketbook
Arcidens confragosus (Say, 1829)
(Plate 3-13)

Arcidens confragosus (Say):
  Parmalee (1967:51; 1962:9)
  Danglade (1914:10)
  MCZ
Alasmodonta confragosa Say:
  Kelly (1899:401)
  Forbes & Richardson (1913:533)
Arcidens confragosus Say:
  Baker (1906:74)
  Morrison (pers. comm., 4 January 1968)
Arcidens confragosa (Say):
  FMNH

Seventy-five live specimens of this species were taken in the 1966 survey of the Illinois River (Table A-3). The rock pocketbook constituted 1.8 percent of the live mussels taken and ranked sixth in abundance (Tables 6 and 7). In the 1966 collections 77.3 percent of all live specimens of this species were taken in the Alton pool. Only one live specimen was collected in the Peoria pool. As indicated in Table A-3, the rock pocketbook was not taken in the Peoria-Pekin area nor upstream from Middle Peoria Lake, which indicated that it was not as tolerant of pollution as some other species. Subfossil shells were collected in 1966 as far upstream as river mile 219.4 (near Spring Valley). A few specimens of this mussel were observed in sorted commercial shell piles at Meredosia and Kampsville.

In the 1966 survey 26.6 percent of the rock pocketbooks taken alive were 2.5 inches or more in height and 77.3 percent were 7–11 years of age (Table A-19). This species was not abundant enough to be of commercial importance.

Calkins (1847:46) did not mention that he had collected this species (*Margaritana confragosa* Say) in the river (Starved Rock pool). However, Baker (1906:74) reported that a specimen of *Arcidens* was collected at Utica, only a short distance downstream from Starved Rock. In 1912 Forbes & Richardson (1913:533) took this species upstream as far as Hennepin. According to Danglade (1914:37 & 42), the rock pocketbook was found on almost all of the mussel beds that he inspected between Henry and Grafton. He regarded this mussel as not particularly useful as a button shell.

Evidently this species formerly was found upstream as far as Utica and was limited by pollution in the 1920's to approximately its present distribution in the river.

The host fish for this mussel is not known.

Museum Records.—Peru (pre-1910) MCZ; between Peoria and Pekin (1908 Freeland & Williams) USNM 677291; Liverpool (pre-1900 Strode) FMNH 9243; Quiver Lake (1894 Baker) UIMNH 22161, (1899) INHS A-99, and (1955 Parmalee) ISM 1054–1066; Havana (Hay) FMNH 13938, (1910 Zetek) FMNH 68169, and (1912) INHS A-140; Frederick (pre-1943 Webb Coll.) FMNH 21646; Meredosia (1930 Morrison) USNM 678629–678630, (pre-1910) MCZ, and (1955 Parmalee) ISM 1392–1393; Naples (1955 Parmalee) ISM 1096–1098; Pearl (1907 F & W) FMNH 11253 and (1965 Parmalee) ISM 3300–3303; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678551; and 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678552.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB), 10.3–10.5 (RB), 14.9–15.1 (RB), 19.2–19.4 (RB), 24.2–24.4 (LB), 28.9–29.1 (RB), 39.1–39.3 (RB), 40.3–40.5 (RB), 42.2–42.3 (LB), 45.4–45.9 (LB), 48.3 (RB), 51.0–51.3 (RB), 51.2 (LB), 53.8 (LB), 54.3 (RB), 56.3 (LB), 57.5–57.7 (LB), 60.8 (RB), 64.4 (LB), 75.8 (RB), 86.4 (LB), 86.6 (LB), 86.8 (LB), 87.9 (LB), 106.7 (LB), 110.0 (RB), 110.5 (RB), 122.0 (LB), 129.8–130.4 (RB), 132.0 (LB), and 167.5–167.7 (LB). OSM 17700–17703, 17704 (2), 17710, 17716, 17717, and 17719; FMNH 156985 (2), 156986 (2), 156988 (4), 157003 (4), and 157006 (9).

Old Shell Records (1966 Survey).—River mile 44.9, 75.8, Quiver Lake, 129.8, 156.0, and 219.4. OSM 18201, 18256, 18304, 18316, 18365, and 18461.

Fluted Shell

Lasmigona costata (Rafinesque, 1820)

Lasmigona costata (Rafinesque):
Parmalee (1967:53)
Margaritana rugosa Barnes:
Calkins (1874:46)
Symphynota costata Rafinesque (= *rugosa* Barnes):
Baker (1906:74)
Symphynota costata (Raf.):
Danglade (1914:10)

According to Baker (1928:143) the fluted shell occurred in both large and small rivers and had a preference for gravel on riffles but also lived in sand and fine gravel in quiet waters. In the early 1870's the Illinois River in the vicinity of Starved Rock had a sandy bottom which supported a large mussel population (Calkins 1874:11). Calkins (1874:46) reported that the fluted shell occurred abundantly there (Starved Rock pool) in the early 1870's, and from the nearby Fox River (a tributary stream of the Illinois) he collected a specimen (USNM 58168) which was deposited at the U.S. National Museum (Morrison, pers. comm., 14 June 1968).

Baker (1906:74) reported that both Handwerk and Strode had collected this species from the river. The last reported record of the fluted shell from the Illinois known by the author was that of a single specimen taken at Bath by Danglade (1914:42) in 1912.

The author was unable to locate a museum specimen of this species from the Illinois. Van der Schalie (pers. comm., 31 August 1967) and Parmalee (pers. comm., 29 June 1967) were of the opinion that the fluted shell could have occurred in the Illinois River. Stansbery (pers. comm., 31 July 1968) informed the author that he would have expected this species to have occurred in the upper reaches of the Illinois before the river was impounded. Morrison (pers. comm., 4 January 1968) had this to say about the fluted shell:

> "Uncommon in the Wisconsin and Rock Rivers; if ever living in the main Illinois River, it must have been in the neighborhood of the Kankakee, before being polluted out."

In 1924 Morrison (Ibid.) collected a living specimen from the Kankakee River at Wilmington (USNM 678623) and a dead shell from the Des Plaines River at Des Plaines (USNM 678624) in 1932. The author examined a fluted shell taken by Hinkley (UIMNH 14801) from the Des Plaines River. The confluence of the Des Plaines and Kankakee rivers is only about 40 miles upstream from where Calkins (1874:46) found the fluted shell occurring abundantly in the early 1870's.

In the author's opinion the citations presented above indicate that the fluted shell formerly occurred in the Illinois River. Pollution probably eliminated this mussel from the upper river, possibly even before the completion of the Chicago Sanitary and Ship Canal in 1900.

The host fish for the fluted shell is not known.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Lasmigona compressa (Lea, 1829)

Lasmigona compressa (Lea):
Parmalee (1967:52)
Symphynota compressa Lea (= *pressa* Lea):
Baker (1906:74)

Baker (1906:74) reported that Handwerk collected this species in the Illinois River. This was the only record of this species from the Illinois known to the author, and he was unable to locate a museum record to substantiate it.

This species, according to Baker (1928:141), was found in creeks, in small streams, and far up into the headwaters of rivers. Morrison (pers. comm., 27

November 1967) and Stansbery (pers. comm., 31 July 1968) were of the opinion that *compressa* probably never had occurred in the Illinois River but rather in its tributary streams.

The author believed that Handwerk's specimen probably was collected either in or near the mouth of a tributary stream of the Illinois rather than from the river proper.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

White Heel-Splitter

Lasmigona complanata (Barnes, 1823)
(Plate 2-12)

Lasmigona complanata (Barnes):
  Parmalee (1967:52)
  Richardson (1928:457)
  MCZ
Margaritana complanata Barnes:
  Calkins (1874:46)
Alasmodonta complanata Bar.:
  Kelly (1899:401)
Symphynota complanata Barnes:
  Baker (1906:75)
  Forbes & Richardson (1913:529)
Symphynota complanata (Barnes):
  Danglade (1914:10)

Calkins (1874:46) considered this mussel abundant in the Illinois River in La Salle County (Starved Rock pool). In the 1896-1897 period, Kelly (1899:401) examined 11 specimens from the Havana area. Danglade (1914:42) considered this mussel fairly common in the Illinois River. In 1912 Forbes & Richardson (1913:528–533) collected specimens upstream as far as Starved Rock, and they took 23 live white heel-splitters at Hennepin in that year.

Richardson (1928:456–457) found in the mid-1920's that the upstream range of this species in the Illinois River had been reduced considerably since 1912 as a result of pollution. He took no live specimen above the lower end of Upper Peoria Lake. This was approximately the location (river mile 168.5) where the last live specimen of this species was taken in the 1966 survey.

In 1966 only 13 live white heel-splitters were taken from the entire river (Table A-3). This species ranked 14th in abundance, based on the total number of live mussels taken (Tables 6 and 7), and it constituted 0.3 percent of the total catch (Table A-3). This species had no importance as a commercial shell from the Illinois River in 1966.

Morrison (pers. comm., 27 November 1967) did not collect this species at Meredosia in 1930. However, in 1957 Parmalee (pers. comm., 21 November 1966) took a live specimen at Liverpool (river mile 128.0) and in 1965 another at Pearl (river mile 43.0). In 1955 he did not find live specimens of this species at Naples or Mededosia (Alton pool).

Evidently, the upstream distribution of the white heel-splitter has been limited by pollution since the 1920's to about the lower end of Upper Peoria Lake. This mussel apparently was much more abundant before 1913 than it was in 1966.

The fish host of the white heel-splitter is not known.

Museum Records.—Peru (pre-1910) MCZ; Liverpool (1957 Parmalee) ISM 2255; Quiver Lake (1955 Parmalee) ISM 1039 (dead); Havana (1909) INHS and (1912) INHS a-208; Naples (1955 Parmalee) ISM 1118 (dead); and Pearl (1965 Parmalee) ISM 3299.

Live Mussel Records (1966 Survey).—River mile 14.9–15.1 (RB), 64.4 (LB), 68.6 (RB), 110.1 (LB), 122.0 (LB), 129.8–130.4 (RB), 145.7 (RB), 148.5 (LB), 161.1–161.3 (LB), 165.3–166.1 (RB), and 168.1–168.5 (RB). OSM 17724; FMNH 156961 and 156998.

Old Shell Records (1966 Survey).—River mile 129.8 and 156.0. OSM 18317 and 18366.

Floater

Anodonta grandis Complex

Anodonta grandis Say:
  Parmalee (1967:47; pers. comm., 21 November 1966)
  Forbes & Richardson (1913:533)

Anodonta ovata Lea:
(Calkins 1874:47)
Anodonta grandis Say (= *salmonia* Lea, *ovata* Lea):
Baker (1906:72–73)
Anodonta grandis (Say):
Danglade (1914:10)
Anodonta grandis var. *gigantea*:
Richardson (1928:457)
Anodonta (Pyganodon) grandis Say:
Morrison (pers. comm., 4 January 1968)
Anodonta (Anodonta) grandis grandis:
FMNH
Anodonta corpulenta Cooper:
Parmalee (1967:47; pers. comm., 21 November 1966)
Calkins (1874:47)
Strode (1891*a*: 133–134)
Kelly (1899:401)
Baker (1906:73)
Forbes & Richardson (1913:525)
Richardson (1928:457)
Anodonta corpulenta (Cooper):
Danglade (1914:10)
Anodonta (Pyganodon) corpulenta Cooper:
Morrison (pers. comm., 4 January 1968)

One hundred twenty live specimens belonging to this complex were taken from the Illinois River in the 1966 survey. The author was unable to identify the species of many of the specimens in this collection. At the suggestion of Dr. David Stansbery the entire collection was submitted to him for study and identification. Dr. Stansbery's analysis of this material (pers. comm., 12 September 1967) follows:

> "The relationship of *Anodonta grandis* Say, 1829, to many of the other *Anodonta* 'species' of North America is unknown. Clarke (1966) has recently studied the *Anodonta cataracta* complex of central and eastern Canada and has concluded that all of the described forms of this complex in the east are reducible to one species having but two subspecies. The *Anodonta grandis* forms of central Canada, he concludes, are all reducible to a single species having but two subspecies (represented in Canada). The task now remains to deal with the relatively few forms of this complex presently recognized in the Mississippi River drainage of central North America. Once accomplished, this should set the stage for dealing with the east and west Gulf Coast (stream) faunas and the lower Atlantic Coast fauna of this complex.
>
> "Simpson (1914) placed most of the *grandis*-like forms described from the Mississippi River drainage into the synonymy of *A. grandis.* Most students of the naiads have been content to let them remain so. Only the *Anodonta* forms of the lakes and big rivers have persisted in the literature into the present as separate species and/or subspecies depending on the author. Baker (1928) was the last author to deal with the big-river *Anodonta* forms in any detail. He recognized *Anodonta grandis* Say, 1829, *Anodonta gigantea* Lea, 1834, and *Anodonta corpulenta* Cooper, 1834, as separate species. These are the only three forms of the complex with which we are concerned in identifying the Illinois River specimens.
>
> "Simpson (1914:420) concludes that *gigantea* Lea is a variety of *A. grandis* and Baker (1928:163) notes that 'Apparently the only sure way of separating *grandis* from *gigantea* is by an examination of the glochidia.' These observations supplemented by a careful examination of the material in the OSM collections lead me to conclude that *gigantea* is most probably the environmental form of *A. grandis* in large rivers. It is larger, more compressed, has a straighter ventral margin, (all relative intergrading characters) and larger glochidia. This latter character (size of glochidia) is the only distinct difference and its dis-

tinctness may well be due to lack of data from populations which are geographically intermediate.

"Although *Anodonta corpulenta* is also known from large rivers or their bayous (as is *A. g. gigantea*), until I examined the Illinois River specimens I saw no cause for confusing the two. Baker (1928:169) notes that *A. corpulenta* 'may be at once known from *grandis gigantea,* which it most nearly resembles, by its large corpulent shell, alate dorsal margin, on both sides of the umbones, its swollen umbones, and its nodulous beak sculpture. It is a squarish shell, the height being almost equal to the length. The glochidia are also different, ...' To these characters I would only add that the nacre is usually a coppery-pink and that the umbonal swelling is best described as mammae-form.

"The Illinois River material (120 specimens) of this complex here under study consists of 119 measurable specimens and one so badly damaged that its dimensions could not be taken. These specimens constitute 47 lots. The dimensions of length, width and height were taken from each specimen and the height index, width index, and transverse index were calculated for all specimens as well as for the types where possible (i.e., no width is given by Cooper (1855) for the type of *A. corpulenta).*

"In height index the type of *A. grandis* (HI = 67) is 5% greater than the type of *A. gigantea* (HI = 62) but only 5% less than the type of *A. corpulenta.* In width index the type of *A. grandis* (WI = 44) is 1% greater than the type of *A. gigantea* (WI = 43). Neither can be compared with the same proportion of the type of *A. corpulenta* since no width dimension or figure of the type was given by Cooper. One is led to believe from the descriptions that *A. corpulenta* is the widest or most corpulent of the complex. Cooper noted that his species is 'much inflated at the umbones, ...' Marsh (1887:36) says *A. corpulenta* is 'very much inflated . . . .' Simpson (1914:430) observes this species 'with excessively full and high beaks, the wide umbonal swelling extending down on the disk . . . .' and Baker (1928: 169) comments on 'its large corpulent shell . . . .' in comparing it with *A. grandis* and *A. gigantea.*

"Marsh (1887:36) in his paper on the shells of Mercer County, Illinois, reveals a broader concept of *A. corpulenta* than most. He states at the close of his description of that species that 'Although *corpulenta* is generally very much inflated, specimens are *often* found that are *much* depressed.' (The underlining is mine.) Earlier Marsh (1887:21) wrote, '*Grandis* is the type of a number of . . . very closely allied species, ... Typical forms of these species are easily separated when once well known, but intermediate forms are so extremely puzzling that no conchologist can separate them to a certainty.' My respect for Marsh has increased markedly since studying the material from the Illinois River!

"Having concluded that *A. gigantea* is most probably an environmental form of *A. grandis* we are left with the relationship between *A. grandis* (and its many forms) with *A. corpulenta.* The Illinois River specimens have a width index extending from a low of 35 to a high of 51 with a mean of 41.5. This mean is slightly less than the mean of the types of *A. grandis* and *A. gigantea.* Thus *A. corpulenta* appears corpulent not because the shell is wider than *A. grandis* or *A. gigantea* but because the shell is narrower both anterior and posterior to the central swelling. I therefore conclude that the width index cannot be used to separate *A. corpulenta* from the others.

"An examination of all of our material of this complex leads me to conclude that *A. corpulenta* is characterized by:

1) having a peculiar expansion of the umbonal region usually extending to the very beaks, which can best be termed mammae-form.
2) a nacre which is copper-pink.
3) a greater height index than related forms.

"Two of these characters (1 and 3) seem to intergrade by imperceptible degrees with *A. grandis* which lacks the mammae-form umbones, is more elongate, and rarely (if ever—never in my experience) has a copper-pink nacre. This intergradation seems, at the present time to be limited to the Illinois River material. Material from the Mississippi River and the lower Tennessee River does not intergrade with *A. grandis.* We have very few specimens of *A. corpulenta* from the Tennessee River, however, and none which fit the description of *A. grandis.*

"The fact that *A. corpulenta* is *not* simply an environmental form of *A. grandis* has been dramatically demonstrated here in Ohio. Until 1966 there were no Ohio records for this species. A draw-down of Cowan Lake, an impoundment of Cowan Creek, revealed an extremely large population of *A. corpulenta.* This is especially noteworthy since Ohio has many such impoundments in which are found populations of *A. grandis* or no naiads at all. Although *A. imbecillis* is present in Cowan Lake, *A. grandis* seems to be completely absent. I believe this to be expected if there are no intrinsic reproductive barriers between the two forms. One would expect the few *A. grandis* specimens present in Cowan Creek to have either been eliminated by the new environment or absorbed by the *A. corpulenta* population. Introductions of bait fishes from the west and elsewhere have been and are being made in Cowan Lake allowing ample opportunity for the introduction of naiad species as encysted glochidia.

"It appears that, under certain conditions, *A. corpulenta* and *A. grandis* can and do live in the same habitat and may intergrade. The Illinois River seems to be just such a situation. Here we find *A. corpulenta* as the common form but accompanied by specimens which deviate in nacre color, height index, and umbonal swelling. Of the 119 specimens studied 101 were *A. corpulenta* in every respect. Fourteen of the 18 additional specimens exhibited mixed characters and are interpreted as intergrades. Only 4 specimens possessed all the characters of *Anodonta grandis.* In view of this evidence, I believe it best to treat *corpulenta* Cooper, 1834, as a subspecies of *grandis* Say, 1829.

Hence:

Anodonta grandis grandis Say, 1829.
—a subspecies of ponds, lakes, and all but the largest rivers.

Anodonta grandis corpulenta Cooper, 1834.
—a subspecies of the bayous and ponded parts of our largest rivers until recently. Now turning up in impoundments *as it has access* to this newly formed favorable habitat."

The author has accepted Dr. Stansbery's opinion that *corpulenta* should be treated here as a subspecies of *grandis.* Since the classification of this complex has been modified here, the author believed that it would be more accurate to list the synonymies of names used by other collectors of *grandis* and *corpulenta* from the Illinois River under the heading of *Anodonta grandis* complex rather than to attempt to allocate them to subspecies. The museum records from the Illinois River have been treated similarly. The old records of *A. grandis* from the river were more questionable, in the author's opinion, than those of *A. corpulenta*. Possibly some of the *A. grandis* specimens reported from the river were intergrades between *grandis* and *corpulenta*, as was the case with 14 of the specimens taken in the 1966 survey.

Calkins (1874:47) reported collecting *A. ovata* and *A. corpulenta* from the Illinois in La Salle County in the early 1870's (Starved Rock pool). At Ottawa in 1912 Forbes & Richardson (1913: 525 & 533) collected a specimen of *A. corpulenta* which "had quite recently succumbed, the flesh being not yet decayed." At Hennepin in that year they took 14 live specimens of *A. corpulenta* and 1 dead *A. grandis*. Richardson (1928:456–457) found that the distribution of *A. corpulenta* had been reduced, as a result of pollution, from as far upstream as Spring Valley in 1912 to no farther up than the lower end of Upper Peoria Lake in the 1924-1925 period. In that period he did not collect *A. grandis* var. *gigantea* from Peoria Lake. Strode (1891*a*:134) found *A. corpulenta* occurring abundantly in the shallow waters of Thompson Lake (now drained and leveed off from the Illinois River) near Havana. In the early 1930's Morrison (pers. comm., 4 January 1968) collected *A.* (*P.*) *grandis* and *A.* (*P.*) *corpulenta* at Meredosia.

Concerning floaters (*Anodonta*) in the Illinois, Danglade (1914:42) stated that:

> "They are thin, paperlike shells and have no commercial or economic value, excepting perhaps as they are used occasionally by the mussel fishermen for fish bait or hog feed"

Museum Records.—(Referred to as *A. grandis*) Between Peoria and Pekin (1908 Freeland & Williams) USNM 678589; between Pekin and Havana (1907 F & W) USNM 677058; Liverpool (1957 Parmalee) ISM 2256 and 2367–2369; Quiver Lake (1955 Parmalee) ISM 1022–1027; Lake Chautauqua (1952) FMNH 54890 and 54898; Thompson Lake (pre-1900 Strode) FMNH 67959; Havana (1894 Baker) UIMNH 22168; Meredosia (1932 Morrison) USNM 678627 and (1955 Parmalee) ISM 1371–1372; Naples (1955 Parmalee) ISM 1099–1102; and Illinois River without locality (1895 Hay) FMNH 6515, (pre-1900 Strode) FMNH 9252, (pre-1943 Webb Coll.) FMNH 21633, and (pre-1910) MCZ.

(Referred to as *A. corpulenta*) Thompson Lake (pre-1900 Strode) FMNH 9251 and 9256 and UIMNH 15038; backwater slough 1 mile W of Havana (1953 Parmalee) ISM 269; Havana (1912) INHS A-145; Meredosia (1930 Morrison) USNM 678628; and Illinois River without locality UIMNH 7366.

(Referred to as possible *A. corpulenta*) Quiver Lake (1955 Parmalee) ISM 1028.

Anodonta grandis grandis Say, 1819
(Plate 1-1)

Only four live specimens of *grandis* were taken in the 1966 survey of the Illinois (Table A-3). All of these mussels were collected in the La Grange and Peoria pools between river miles 100.0 and 196.1, including one specimen from Quiver Lake. In the author's opinion this subspecies was never as abundant in the Illinois River and its bottomland lakes as *corpulenta*.

According to Parmalee (1967:100), the host fishes for *A. grandis* are the carp, *Cyprinus carpio* Linnaeus, yellow perch, bluegill, rock bass, and white crappie. All of these fishes are common in the Illinois River proper except the rock bass and yellow perch.

Museum Records.—Utica (pre-1900) OSM 9085; and Illinois River without locality (pre-1900) OSM 10403.

Live Mussel Records (1966 Survey).—River mile 100.0–100.5 (LB), Quiver Lake (LB), 167.2 (RB), and 196.1 (LB).

OSM 17430, 17435, 17447, and 17461.

Old Shell Records (1966 Survey).—None.

Anodonta grandis corpulenta Cooper, 1834
(Plate 1-2)

The *corpulenta* subspecies was distributed throughout the lower three navigation pools of the Illinois River in 1966 (Table A-3); 116 live specimens were taken. *Corpulenta* ranked fifth in abundance in the 1966 collections of live mussels from the entire river, and in the Peoria pool it ranked second in abundance (Tables 6 and 7).

The occurrence of *corpulenta* in the upper parts of the La Grange and Peoria pools indicated that it was one of the species more tolerant of pollution than other mussels. The reports and records on the *A. grandis* complex presented above indicated that *corpulenta* formerly occurred upstream at least as far as Ottawa and that by the 1920's its upstream distribution had been reduced considerably by pollution. The 1966 survey data indicated that this mussel now occurs farther upstream than it did in the 1920's, as reported by Richardson (1928:456–457).

Baker (1928:169) states that the skipjack is the host fish for *corpulenta.* The author is of the opinion that perhaps some other kind or kinds of fishes besides the skipjack serve as hosts for this mussel. This opinion is based on the fact that the skipjack is uncommon in the Illinois River, whereas *corpulenta* is common and widely distributed in the lower three navigation pools.

Museum Records.—Utica (pre-1900) OSM 9086; and Illinois River without locality (pre-1900) OSM 10397 and 23992 (dead).

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 5.4–5.5 (RB), 13.0 (RB), 13.2–13.5 (LB), 14.9–15.1 (RB), 29.0 (RB), 30.6 (RB), 53.6 (LB), 66.0–66.4 (LB), 68.6 (RB), 75.8 (RB), 86.8 (LB), 106.7 (LB), 110.0 (RB), 115.5 (RB), 122.0 (LB), 129.8–130.4 (RB), 143.7 (RB), 145.7 (RB), 147.7 (RB), 148.5 (LB), 155.9–156.4 (RB), 161.2 (RB), 161.7–161.8 (LB), 162.3 (RB), 162.3 (LB), 164.4–165.1 (LB), 164.5–164.9 (RB), 166.6 (LB), 167.5–167.7 (LB), 168.1–168.5 (RB), 168.2 (RB), 169.3 (RB), 169.5 (LB), 170.5–170.9 (LB), 170.9 (RB), 174.1 (LB), 174.9 (LB), 191.5 (LB), 196.1 (LB), 198.1 (RB), and 229.3 (LB). OSM 17417 (5), 17418 (7), 17419 (6), 17420–17425, 17426 (11), 17427, 17428 (2), 17429, 17431 (3), 17432–17434, 17436 (10), 17437, 17438 (4), 17439 (3), 17440–17442, 17443 (2), 17444, 17445, 17446 (2), 17448 (2), 17449 (9), 17450, 17451 (2), 17452 (4), 17453 (7), 17454 (2), 17455 (2), 17456, 17457 (4), 17458 (2), 17459 (½), 17460, 17461 (3), 17462, and 17463.

Old Shell Records (1966 Survey).—River mile Meredosia Lake, 66.0–66.4, 75.8, 86.6–86.8, Lake Matanzas, Quiver Lake, 129.8, 156.0, and 184.5. OSM 18263, 18274, 18367, and 18383.

Paper Pond Shell
Anodonta imbecillis Say, 1829
(Plate 2-8)

Anodonta imbecillis Say:
  Parmalee (1967:48)
  Calkins (1874:47)
  Baker (1906:72)
  Forbes & Richardson (1913:533)
  Richardson (1928:457)
  MCZ
Anodonta imbecilis Say:
  Kelly (1899:401)
Anodonta imbicillis (Say):
  Danglade (1914:10)
Anodonta imbecillis (Say):
  Danglade (1914:43)
Anodonta (*Anodonta*) *imbecilis* Say:
  Morrison (pers. comm., 4 January 1968)

Regarding the paper pond shell in the Illinois River, Danglade (1914:43) stated: "This small, delicate shell is very abundantly distributed, especially in the more retired places of quiet waters." However, he indicated (1914:37) that this shell was taken only at three of his principal stations (Peoria Lake, Havana, and Bath). Calkins (1874:47) reported collecting this mussel in La Salle County (Starved Rock pool) in the early 1870's, but in 1912 Forbes & Richardson (1913: 533) found it occurring upstream only as far as Hennepin. By the mid-1920's Richardson (1928:457) found that its upstream range was limited to the lower end of Upper Peoria Lake as a result of pollution. Kelly (1899:401) examined 47 specimens of this mussel from the river at Havana in the 1896-1897 period, and in 1930 Morrison (pers. comm., 4 January 1968) collected it at Meredosia.

In the 1966 survey ony five live paper pond shells were collected at four different sites between river miles 30.6 and 198.1 (above Henry) (Table A-3). These specimens were collected by wading and with the dredge; they were 4–7 years of age. This species was apparently less abundant in the Illinois River in 1966 than it was before 1913; however, it had moved upstream since the mid-1920's.

The fish host for this mussel is *Lepomis* sp. (Parmalee 1967:100).

Museum Records.—Peru (pre-1910) MCZ; Depue Lake (1918 Baker) UIMNH 10982; Mossville (1924) INHS G-5-A; Peoria Lake (1931 Baker) UIMNH 31487 and 31531–31532; Quiver Lake (1955 Parmalee) ISM 1030 and 1038; and Merdeosia (1930 Morrison) USNM 678625–678626.

Live Mussel Records (1966 Survey).—River mile 30.6 (RB), 66.0–66.4 (LB), 129.8–130.4 (RB), and 198.1 (RB). OSM 17743 and 18021.

Old Shell Records (1966 Survey).—None.

Heel-Splitter
Anodonta suborbiculata Say, 1831
(Plate 4-19)

Anodonta suborbiculata Say:
Parmalee (1967:48)
Strode (1891*a*:133)
Baker (1906:72)
Richardson (1928:457)
Anodonta suborbiculata (Say):
Danglade (1914:10)
Anodonta (*Utterbackiana*) *suborbiculata* (Say):
FMNH

In 1890 at Thompson Lake (now drained and leveed off from the river) near Havana, Strode (1891*a*: 133–134) noted:

> "In some places the bottom of the lake seemed to be literally paved with the suborbiculata. With a six-tined potato-digger I would sometimes bring up five or six at a haul; and if the fishermen happened to be making a draw with the great seine, a half barrel of them would sometimes be drawn out at once . . ."

Danglade (1914:37 & 43) collected the heel-splitter from the river at Peoria Lake, Havana, Bath, and Bedford. He mentioned that it was widely distributed in the Illinois and was generally found on mud bottoms in slack water. In the 1924-1925 period Richardson (1928: 457) reported taking this mussel in Middle Peoria Lake. In 1953 Parmalee (pers. comm., 21 November 1966) found the heel-splitter occurring commonly in a mud slough backwater area of the Illinois River near Havana.

In the 1966 survey *suborbiculata* was not taken from the river proper; however, one living specimen was collected from Lake Matanzas, a river bottomland lake located south of Havana.

The host fish for this mussel is not known.

Museum Records.—Mossville (1924) INHS E-5a; Thompson Lake (pre-1900 Strode) FMNH 2574, 9254, 50232, and 68176 and (Hinkley) UIMNH 4709; Havana (1894) INHS and (1894 Baker) UIMNH 22162; 1 mile W of Havana in a backwater slough of the Illinois River (1953 Parmalee) ISM 61–63, 89, and 260.

Live Mussel Records (1966 Survey).—Lake Matanzas (LB). OSM 17723.

Old Shell Records (1966 Survey).—None.

Slipper-Shell
Alasmidonta calceolus (Lea, 1829)

Alasmidonta calceolus (Lea):
Parmalee (1967:44)
Baker (1928:187)
Margaritana deltoidea Lea:
Calkins (1874:46)
Alasmidonta viridis Rafinesque, 1820:
Morrison (pers. comm., 14 June 1968)

This small-stream species was reported

by Calkins (1874:46) as occurring in the Illinois River. This report was corroborated by Dr. Morrison (pers. comm., 14 June 1968), who wrote that he had examined in the collections of the U.S. National Museum a specimen of *Alasmidonta viridis* Rafinesque collected from the Illinois River by Calkins. He mentioned that the specimen was labelled "*deltoidea.*" Neither Baker (1906) nor Danglade (1914) reported the slipper-shell from the Illinois. However, at a later date Baker (1928:187) stated that this species did occur in the Illinois, but he made no mention of locality or collector. Apparently this species formerly occurred only in limited numbers in the upper river and was eliminated from the river about 1900 by pollution.

The host fish for the slipper-shell is not known.

Museum Records.—Illinois River without locality (1870's Calkins) USNM 26047.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Elk-Toe

Alasmidonta marginata Say, 1818

Alasmidonta marginata (Say):
    Parmalee (1967:45; 1962:9)
Margaritana marginata Say:
    Calkins (1874:46–47)
Alasmidonta marginata Say:
    Baker (1906:75)
    Morrison (pers. comm., 14 June 1968)
Alasmidonta (*Decurambis*) *marginata* (Say):
    FMNH

According to Calkins (1874:46–47) the elk-toe occurred abundantly in the upper river in the early 1870's. Baker (1906:75) reported than Handwerk also had collected this species from the river. Parmalee (1962:7 & 9) found the elk-toe in the Kingston Lake Site middens along the Illinois River (15 miles SW of Peoria); however, he thought that the finding of this headwater or small-stream species was unusual, since all other mussel specimens at the site were large-river species. Dr. Morrison (pers. comm., 14 June 1968) mentioned that in the collections of the U.S. National Museum are specimens of this species taken before 1900 from the Illinois River at Morris and Peoria.

The author was unable to find any record of the elk-toe from the Illinois after the turn of the century. Apparently this species formerly occurred only in the upper and middle parts of the Illinois and was eliminated by pollution following the opening of the Chicago Sanitary and Ship Canal in 1900.

The host fish of the elk-toe is not known.

Museum Records.—Morris (pre-1900 Shimek Coll.) USNM 504536; Peoria (1875 Lewis) USNM 86177; and Illinois River without locality (pre-1943 Webb Coll.) FMNH 21703.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Squaw Foot

Strophitus undulatus (Say, 1817)

Strophitus rugosus (Swainson):
    Parmalee (1967:56)
    Baker (1928:201)
Strophitus edentulus Lea:
    Kelly (1899:401)
    Forbes & Richardson (1913:530 & 533)
Strophitus edentulus Say (= *shafferiana* Lea, *wardiana* Lea):
    Baker (1906:71)
Strophitus edentulus (Say):
    Danglade (1914:10)
Strophitus undulatus (Say):
    Morrison (pers. comm., 4 January 1968)

Danglade (1914:43) reported that the squaw foot was: "Found rather scattering throughout the various stretches and mussel beds of the river." He (1914:37) collected this mussel at Peoria Lake, Pekin, Bath, Florence, and Hardin. In 1912 Forbes & Richardson (1913:530 & 533) collected a dead shell of this mussel in the La Salle-Peru area and a live specimen at Hennepin. Neither Morrison (pers. comm., 4 January 1968) in the early 1930's nor Parmalee (pers. comm., 29 June 1967) in the 1950's took the squaw foot in the Illinois River.

The squaw foot was not taken in the

1966 Illinois River survey; however, a live specimen (OSM 18183, identified by Dr. Stansbery as *Strophitus undulatus* Say, 1817)[1] was collected in 1966 from the Aux Sable River, a tributary stream of the Illinois.

This species was evidently never common in the Illinois River and it probably disappeared from the river before 1930.

According to Baker (1928:201), the glochidia of this mussel have experimentally gone through metamorphosis on the fins and skin of the largemouth bass and the creek chub, *Semotilus atromaculatus* (Mitchill). Both of these fishes occur in the Illinois River.

Museum Records.—Havana (Smith) UMMZ 74648 and (1894 Baker) UIMNH 22170; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678553; Illinois River without locality (1907 Freeland & Williams) USNM 678590 and INHS.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Cylindrical Paper Shell

Anodontoides ferussacianus (Lea, 1834)

Anodontoides ferussacianus (Lea):
    Parmalee (1967:51)
    MCZ
Anodontoides ferrussacianus [sic]:
    Forbes & Richardson (1913:533)
Anodontoides ferrusacianus [sic]:
    Richardson (1928:457)

> "This small, rather fragile, thin-shelled mussel is found mainly in the northern third of the state [Illinois], living in small, quiet streams, on a sand or fine gravel bottom in shallow water" (Parmalee 1967:51).

Forbes & Richardson (1913:533) reported collecting a live specimen of this species from the Illinois River at Hennepin in 1912. Two unmatched valves of this species taken from the river at Peru (pre-1910) were deposited in the Museum of Comparative Zoology. Dr. Stansbery (pers. comm., 20 January 1970) checked these shells for the author and found them to be typical *Anodontoides ferussacianus.*

This small-stream species was not collected in the 1966 survey of the river. The paucity of records for this species from the Illinois indicated that its occurrence there was probably accidental even before 1900.

The host fish of this mussel is not known.

Museum Records.—Peru (pre-1910) MCZ 70919.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Subfamily LAMPSILINAE

(von Ihering, 1901) Ortmann, 1910

Three-Horned Warty-Back

Obliquaria reflexa Rafinesque, 1820

(Plate 3-15)

Obliquaria reflexa Rafinesque:
    Parmalee (1967:77)
    Kelly (1899:401)
    Forbes & Richardson (1913:536)
    Richardson (1928:457)
    Morrison (pers. comm., 4 January 1968)
Unio cornutus Barnes:
    Calkins (1874:41)
Obliquaria reflexa Rafinesque (=*cornuta* Barnes):
    Baker (1906:71)
Obliquaria reflexa (Raf.):
    Danglade (1914:10)

According to Danglade (1914:43):

> "This mussel is widely distributed and is usually of small size. There are two or three forms of *reflexa* found in the Illinois. In the upper stretches of the river it is of the ordinary shape and size found in other streams, and although it can be used for manufacturing purposes it is not a particularly valuable shell to propagate. In the Peoria Lake region, however, where the current

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[1] Stansbery (pers. comm., 20 July 1967) stated: "The reason that *S. undulatus* (Say, 1817) has *S. rugosus* (Swainson, 1822) as a synonym is because:
"(1) No one has ever been able to demonstrate that there are indeed two species (one eastern in New York, New England, etc., and one Miss. drainage) and
"(2) *Strophitus undulatus* (Say) has five years' priority as the name of this species. Clarke and Berg (1959:43–44) recognized the conspecificity of *undulatus* Say and *rugosus* Swainson in their study of the naiads of upper New York."

> is slow and the bottom is composed of soft mud, the shell is often very heavy and rounded anteriorly, while posteriorly it is thin and much elongated, which no doubt is the result of accommodation to natural conditions. In the lower stretches the shell, though heavy and inflated, is considerably smaller than those in the upper portions of the river."

In the early 1870's Calkins (1874:41) collected *O. reflexa* from the river in La Salle County (Starved Rock pool). Forbes & Richardson (1913:536) took this mussel as far upstream as the Henry-Chillicothe section in 1912. However, by the mid-1920's the range of this species extended upstream only to Middle Peoria Lake as a result of pollution (Richardson 1928:456–457). In 1912 Danglade (1914:37) collected the three-horned warty-back at Chillicothe, Peoria Lake, and at most of his other principal stations downstream.

In the 1966 survey the three-horned warty-back was taken alive from the river proper only in the Alton pool between river miles 0.9 and 75.8 (Table A-3). A single live specimen was taken by wading in the La Grange pool at Quiver Lake just above Havana. This species ranked seventh in abundance in the Alton pool and tenth in the entire river (Tables 6 and 7). The shell heights ranged from 0.9 to 1.6 inches; these shells were therefore too small to have any commercial importance in the pearl-culture industry. The 49 live three-horned warty-backs taken in the 1966 survey ranged from 4 to 15 years in age, but 87.8 percent of these mussels were 6–11 years old (Table A-20).

Since the early 1870's the range of the three-horned warty-back has been greatly reduced as a result of pollution, and this mussel now occurs only in the lower navigation pool of the river proper.

The fish host of the three-horned warty-back is not known.

Museum Records.—Peoria Narrows (1924) INHS 1-J; Peoria, above bridge (1912 Danglade) USNM 678604; Quiver Lake (1955 Parmalee) ISM 1050–1052; Havana (1894 Baker) UIMNH 22165–22166, (1895 Hay) FMNH 14892, and (1912) INHS a-138; Meredosia (1930 Morrison) USNM 678650 and (1955 Parmalee) ISM 1366–1370; Naples (1955 Parmalee) ISM 1124–1129; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678568; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678569; 2 miles above Grafton (1907 Bartsch stat. 111) USNM 678570; and Illinois River without locality FMNH 22863 and 22873.

Live Mussel Records (1966 Survey).—River mile 0.9–1.0 (LB), 5.5 (RB), 10.5 (RB), 14.9–15.1 (RB), 21.7–22.0 (RB), 29.0 (RB), 40.3–40.5 (RB), 42.3 (LB), 45.4–45.9 (LB), 51.2 (LB), 54.3 (RB), 54.4 (RB), 58.0 (RB), 62.6 (RB), 64.4 (LB), 69.0 (RB), 72.9 (RB), 75.8 (RB), 79.8 (RB), and Quiver Lake (LB). OSM 18017 and 18019; FMNH 156946, 156949, 156967, 156968, 156976 (2), 156990, and 156991 (4).

Old Shell Records (1966 Survey).—River mile 15.0, 44.9, 66.0–66.4, 75.8, 156.0, 196.1, and 219.4. OSM 18202, 18208, 18222, 18257, 18368, 18434, and 18462.

Hickory-Nut
Obovaria olivaria (Rafinesque, 1820)
(Plate 4-20)

Obovaria olivaria (Rafinesque):
  Parmalee (1967:78; 1962:9)
  OSM
Unio ellipsis Lea:
  Calkins (1874:42)
Lampsilis ellipsis Lea:
  Kelly (1899:401)
Obovaria ellipsis Lea:
  Baker (1906:69)
Obovaria ellipsis (Lea):
  Danglade (1914:10)

One live specimen of the hickory-nut was taken in the 1966 survey with the exploratory crowfoot bar on a hard mud bottom in 11.3 feet of water at river mile 1.0. This specimen was 11 years of age and its shell height was 2.0 inches.

In the early 1870's Calkins (1874:42) reported that this species occurred abundantly in the Illinois River in La Salle County (Starved Rock pool). In the 1896-1897 period Kelly (1899:401) examined three specimens of this species taken from the river in the Havana area. Baker (1906:69) mentioned that Handwerk collected the hickory-nut in the Illinois. Danglade (1914:44) considered this species comparatively rare in the river in 1912. At that time he (1914:37 & 44) took a few hickory-nuts at Peoria Lake, Florence, Bedford, Pearl, Kampsville, Hardin, Twelve-Mile Island, and Grafton (possibly Mississippi River).

This species was not taken by Morrison (pers. comm., 4 January 1968) at Meredosia in the early 1930's. He commented that:

> "in 1931 at Fairport, Iowa, in the Mississippi River, this species was almost completely replacing *Sintoxia antrosa* [*ebena*] behind the wing dams on that river."

In the present study only one live specimen of each of these two species was taken from the Illinois River, and both of these records were from near the mouth of the river where it empties into the Mississippi River.

According to Parmalee (1967:78) the hickory-nut occurs: "usually on a sand or gravel bottom in good current." Siltation and pollution probably have been the factors which have virtually eliminated the hickory-nut from the river.

The host fish for the hickory-nut is not known.

Museum Records.—Starved Rock (pre-1900) OSM 10214; Peoria (1870's) BK; and Calhoun County (1928 Baker) UIMNH 27286.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB). OSM 18014.

Old Shell Records (1966 Survey).—None.

Obovaria retusa (Lamarck, 1819)

Obovaria retusa (Lamarck):
Parmalee (1967:94)
Unio retusus Lam.:
Calkins (1874:44)
Obovaria retusa Lamarck:
Baker (1906:69)

Calkins (1874:44) and Strode (Baker 1906:69) both supposedly collected this species from the Illinois River. However, the author was unable to locate any other records of this mussel's having been taken from the Illinois. Concerning this species in Illinois, Parmalee (1967:78) stated:

> "*Obovaria retusa* . . . formerly occurred in the lower Wabash and Ohio rivers, but it has apparently now disappeared from these rivers."

Because of the lack of substantial evidence of the occurrence of this species in the Illinois River, the author considered the above reports of *retusa* doubtful.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Mucket
Actinonaias ligamentina
(Lamarck, 1819)

Actinonaias carinata (Barnes):
Parmalee (1967:56; 1962:9)
MCZ
Actinonais [sic] *carinata*:
Richardson (1928:457)
Unio ligamentinus Lam.:
Calkins (1874:43)
Lampsilis ligamentinus Lam.:
Kelly (1899:401)
Lampsilis ligamentina:
Forbes & Richardson (1913:529)
Lampsilis ligamentina Lamarck (=*crassa* Say):
Baker (1906:65)
Lampsilis ligamentina (Lam.):
Danglade (1914:10)
Actinonaias ligamentina Lamarck, 1819:
Morrison (pers. comm., 4 January 1968)
OSM

No live muckets were taken in the 1966 survey; however, old shells of this species were collected at various points along the entire Illinois River from river mile 44.9 to mile 256.5. In the early 1870's Calkins (1874:43) found this mussel occurring abundantly in the upper river (Starved Rock pool). In 1912 Forbes & Richardson (1913:529) took living muckets as far upstream as the La Salle-Peru area. Richardson (1928: 456–457) reported that by the mid-1920's pollution had eliminated this species from the river, at least from Peoria up.

Before the turn of the century the mucket was common in the Havana area, as evidenced by Kelly's (1899:401) report of examining 24 specimens collected from that part of the river in the 1896-1897 period. In 1912 Danglade (1914:37) collected this species at all of his principal collecting stations between Henry and Grafton with the exception of Meredosia. He (1914:46) found the mucket occurring in small numbers throughout the river but more abundantly in Peoria Lake than elsewhere. Neither Morrison in the early 1930's (pers. comm., 4 January 1968) nor Parmalee in the 1950's (pers. comm., 21 November 1966) collected this species from the river.

Apparently pollution and siltation had eliminated this formerly widely distributed mussel in the Illinois River before 1930.

According to Baker (1928:220) the host fishes for the mucket are: green sunfish; bluegill; smallmouth bass, *Micropterus dolomieui* Lacépède; largemouth bass; yellow perch; white crappie; and white bass. All of these fishes still occur in the Illinois River.

Museum Records.—Peru (pre-1910) MCZ; Peoria (pre-1900) OSM 10232; between Pekin and Havana (pre-1910) MCZ; Havana (1894 Baker) UIMNH 22152 and (1912) INHS A-174; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678571 and (1907 Bartsch stat. 109) USNM 678572; and Illinois River stat. K_2 (1908 Freeland & Williams) USNM 678605.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 44.9, 94.3, 106.8, 129.8, 145.7, 156.0, 196.3–198.1, 219.4, 240.4, and 253.5–256.5. OSM 18205, 18286, 18296, 18318, 18334, 18370, 18464, 18465, 18468, and 18482.

Butterfly
Plagiola lineolata (Rafinesque, 1820)

Plagiola lineolata (Rafinesque):
- Parmalee (1967:80–81; 1962:9)
- Richardson (1928:457)
- MCZ

Plagiola securis Lea:
- Kelly (1899:401)
- Baker (1906:69)
- Forbes & Richardson (1913:536)

Plagiola securis (Lea):
- Danglade (1914:10)

Plagiolopsis lineolata (Raf.):
- FMNH

Ellipsaria lineolata Rafinesque, 1820:
- Morrison (pers. comm., 4 January 1968)

Concerning this species in the Illinois River, Danglade (1914:44) stated:

> "The butterfly, or *securis,* is not a common species in this river, although many of the beds could be made to yield productively by propagation. On account of its flatter shape and proportionally lighter weight, the male shell is more valuable for commercial purposes than the female."

Danglade (1914:37) reported that this species occurred at all of his principal collecting stations except Henry, Bedford, and Spar Island. In 1912 Forbes & Richardson (1913:536) collected the butterfly in the Henry-Chillicothe section of the river; however, in the mid-1920's this species was not taken in Peoria Lake by Richardson (1928:457). Kelly (1899:401) examined five specimens of this mussel collected in the Havana area.

The butterfly was not taken alive in the 1966 survey, nor was it taken by Morrison (pers. comm., 4 January 1968) in the early 1930's nor Parmalee in the 1950's. The literature citations, museum records, and old shell records included here indicated that the butterfly formerly occurred throughout much of the river, but this mussel probably had disappeared by the mid-1920's. Parmalee (1967:81) stated that:

> "*Plagiola* is apparently less tolerant

of silting and pollution than many species; it was once fairly common and widespread in the Illinois River, but has now completely disappeared as a result of these factors."

The fish host for the butterfly mussel is the freshwater drum, *Aplodinotus grunniens* Rafinesque, (Baker 1928:232) still a common fish in the Illinois River.

Museum Records. — Starved Rock FMNH 59280; La Salle (Baker) UIMNH 14073; Peru (pre-1910) MCZ; Peoria (1912) INHS; Fulton County (pre-1900 Strode) FMNH 9217; Havana (1912) INHS; Meredosia (1913) INHS and (pre-1910) MCZ; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678573; and Illinois River without locality (1879 Hinkley) UIMNH 4499 and (1870's) BK.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— River mile 44.9, 156.0, and 219.4. OSM 18204, 18369, and 18463.

Deer-Toe
Truncilla truncata Rafinesque, 1820
(Plate 4-21)

Truncilla truncata Rafinesque:
  Parmalee (1967:86)
  Richardson (1928:457)
  MCZ
Unio elegans Lea:
  Calkins (1874:42)
Plagiola elegans Lea:
  Kelly (1899:401)
  Baker (1906:70)
  Forbes & Richardson (1913:536)
Plagiola elegans (Lea):
  Danglade (1914:10)
Truncilla vermiculata Rafinesque, 1820:
  Morrison (pers. comm., 4 January 1968)
Truncilla truncata (Raf.):
  FMNH

Danglade (1914:37 & 44) found the deer-toe in small quantities in 1912 at all but three of his principal stations between Henry and Grafton. In the early 1870's Calkins (1874:42) took this species in La Salle County (Starved Rock pool). Forbes & Richardson (1913:536) collected the deer-toe in 1912 upstream as far as the Henry-Chillicothe section. Richardson (1928:456–457) reported that by the mid-1920's pollution had eliminated this species from Peoria north. In the 1896-1897 period, Kelly (1899:401) examined 25 deer-toes collected in the Havana area.

In the 1966 survey 10 live deer-toes were taken between river miles 1.0 and 106.7. All but two of these specimens were collected in the Alton pool (Table A-3). The deer-toe ranked 15th in abundance in the 1966 survey (Tables 6 and 7). The heights of the shells of this species ranged from 0.9 to 1.3 inches. Danglade (1914:44) reported that in 1912 he examined a deer-toe from the Illinois which had a shell length of 2.75 inches, whereas the largest shell of this species taken in 1966 had a length of only 2.2 inches, too small to be of commercial value. The deer-toes collected in the 1966 survey ranged from 5 to 9 years in age. Evidently pollution has eliminated the deer-toe from the river proper above river mile 106.7.

The fish host of the deer-toe is not known.

Museum Records. — La Salle (pre-1910) MCZ; Peru (pre-1910) MCZ; Peoria, above bridge (1912 Danglade) USNM 678606; Peoria (1913) USNM 678607; Quiver Lake (1955 Parmalee) ISM 1048; Havana (1894 Baker) UIMNH 22167, (1895 Hay) FMNH 6483, (1912) INHS a-122, and (1912) USNM 678608; Bath (1912) USNM 678609; Grand Island near Bath (1912 Danglade) USNM 678611; Meredosia (1912) USNM 678610, (1930 Morrison) USNM 678651, and (1955 Parmalee) ISM 1385–1386; Naples (1955 Parmalee) ISM 1145–1151; Diamond Island, Dark Chute (1912 Danglade) USNM 678487; Hardin (1912 Danglade) USNM 678612; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678574; and Illinois River without locality (1870's) BK.

Live Mussel Records (1966 Survey).— River mile 1.0 (LB), 64.4 (LB), 72.9 (RB), 75.8 (RB), 100.0–100.5 (LB), and 106.7 (LB). OSM 18015 and 18020; FMNH 156969 (2).

Old Shell Records (1966 Survey).—River mile 15.0, 44.9, 66.0–66.4, 75.8, 94.3, and Quiver Lake. OSM 18203, 18209, 18223, 18285, and 18305.

Fawn's Foot
Truncilla donaciformis (Lea, 1828)
(Plate 4-22)

Truncilla donaciformis (Lea):
  Parmalee (1967:85)
  OSM
Unio zigzag Lea:
  Calkins (1874:46)
Plagiola donaciformis Lea:
  Kelly (1899:401)
Plagiola donaciformis Lea (=*zigzag* Lea):
  Baker (1906:70)
Plagiola donaciformis (Lea):
  Danglade (1914:10)
Truncilla (*Amygdalonaias*) *donaciformis* Lea:
  Morrison (pers. comm., 4 January 1968)

Danglade (1914:43) considered this small mussel very common in the Illinois although he (1914:37) collected it at only about one-half of his principal stations between Henry and Grafton. The museum records indicate that this species once occurred in much of the river between Starved Rock and Grafton. This species was not collected from the Illinois River in 1912 between Morris and Chillicothe by Forbes & Richardson (1913). The farthest upstream the fawn's foot was taken by Danglade (1914:37) in 1912 was Peoria Lake.

In 1930 Morrison (pers. comm., 4 January 1968) took this species at Meredosia. Parmalee (pers. comm., 21 November 1966) in 1955 found the fawn's foot occurring commonly at Naples, Meredosia, and Quiver Lake. In the 1966 survey only one live specimen of this species was taken, and that was collected by wading at Naples. This species probably was too small to be taken with either the crowfoot bar or the dredge; however, if the species had occurred commonly in the river in 1966 it would have been taken regularly in the wading collections.

Evidently by 1912 pollution had eliminated this mussel from the river above Peoria Lake, and by 1966 it had been drastically affected in the lower river. It apparently occurs now only in small numbers in the Alton navigation pool of the river proper.

The freshwater drum is the usual host fish for the fawn's foot (Baker 1928: 230), and this fish still occurs in the river.

Museum Records.—Starved Rock (pre-1900) OSM 10250 and (pre-1923 Ferriss) FMNH 59226; Utica (pre-1923 Ferriss) FMNH 59246; La Salle (Hinkley) UIMNH 14994; Peoria, above bridge (1912 Danglade) USNM 678613; Quiver Lake (1955 Parmalee) ISM 1040–1047; Havana (1894 Baker) UIMNH 22169 and (1912) INHS a-167; Lake Matanzas UIMNH 4542; Meredosia Lake (1909) UIMNH 4523; Meredosia (1930 Morrison) USNM 678652–678653 and (1955 Parmalee) ISM 1387–1391; Naples (1955 Parmalee) ISM 1152–1155; 1 mile N of Hardin (1956 Parmalee) ISM 2206 (dead); and 2 miles above Grafton (1907 Bartsch stat. 111) USNM 678575.

Live Mussel Records (1966 Survey).—River mile 66.0–66.4 (LB). OSM 18018.

Old Shell Records (1966 Survey).—River mile 15.0 and Quiver Lake. OSM 18210 and 18306.

Fragile Paper Shell
Leptodea fragilis (Rafinesque, 1820)
(Plate 2-11)

Leptodea fragilis (Rafinesque):
  Parmalee (1967:72)
  MCZ
Unio gracilis Barnes:
  Calkins (1874:42)
Lampsilis gracilis Bar.:
  Kelly (1899:401)
  Forbes & Richardson (1913:529)
  Baker (1906:68)
Lampsilis gracilis (Barnes):
  Danglade (1914:10)
Lampsilis (*Leptodea*) *fragilis* (Raf.):
  FMNH

Leptodea fragilis Raf.:
Baker (1928:234)
Richardson (1928:457)
Morrison (pers. comm., 4 January 1968)

The fragile paper shell was widely distributed in the lower three navigation pools of the Illinois River in 1966, and 64 live specimens were taken between river miles 1.0 and 229.0 (Table A-3). It ranked eighth in abundance in 1966 (Tables 6 and 7). The shells ranged from 1 to 13 years of age. The 1-year-old shell was taken in the Alton pool and had a height of 0.3 inch. Shells of this species were too thin to be of any commercial value.

In the 1870's Calkins (1874:42) collected this mussel in La Salle County (Starved Rock pool). In the 1896-1897 period Kelly (1899:401) examined 40 specimens of this species collected in the Havana area. Danglade (1914:37) found the fragile paper shell occurring at all of his principal stations between Henry and Grafton except at Valley City, Bedford, and Six-Mile Island. Forbes & Richardson (1913:529) in 1912 collected this species upstream as far as the La Salle-Peru area. By the 1920's pollution had reduced this mussel's upstream range to Middle Peoria Lake (Richardson 1928:457). As indicated above, in 1966 live specimens of the fragile paper shell were taken at river mile 229.0 (above La Salle), farther upstream than it was taken in 1912 by Forbes & Richardson. The apparent reestablishment of this species upstream since 1912 and the mid-1920's indicated that it was capable of adapting to pollution more successfully than most of the mussels known to have occurred in the Illinois River and that pollution was less severe than it was in the 1920's. It was also one of the few mussel species able to survive the pollution in the Peoria-Pekin section of the river.

The host fish for the fragile paper shell is not known.

Museum Records.—Peru (pre-1910) MCZ; between Peoria and Pekin (1908 Freeland & Williams) USNM 678614; Pekin (1907 F & W) FMNH 11224; between Pekin and Havana (1907 F & W) USNM 677057 and (pre-1910) MCZ; Liverpool (1957 Parmalee) ISM 2257–2259; Clear Lake (1894 Baker) UIMNH 22156; Quiver Lake (1894 Baker) UIMNH 22157 and (1955 Parmalee) ISM 1031–1033; 1 mile W of Havana, backwater slough (1953 Parmalee) ISM 88; Havana (1895 Hay) FMNH 14909 and (1912) INHS A-92; Meredosia (1930 Morrison) USNM 678654 and (1955 Parmalee) ISM 1373–1379; Naples (1955 Parmalee) ISM 1103–1108; 1 mile N of Hardin (1956 Parmalee) ISM 2196–2199 (dead); 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678576; and Calhoun County (1928 Baker) UIMNH 27290.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 5.5 (RB), 10.3–10.5 (RB), 13.2–13.5 (LB), 14.9–15.1 (RB), 28.9–29.1 (RB), 47.4–47.7 (LB), 53.6 (LB), 56.3 (LB), 58.0 (RB), 60.8 (RB), 62.4 (RB), 62.6 (LB), 64.4 (LB), 66.0–66.4 (LB), 66.5 (LB), 66.9 (RB), 69.0 (RB), 72.9 (RB), 75.8 (RB), 79.8 (RB), 93.6 (LB), 95.8 (LB), 96.8 (RB), 98.0 (LB), 99.0–99.5 (RB), 100.0–100.5 (LB), 106.7 (LB), 108.8–109.0 (RB), 110.1 (LB), 110.5 (RB), 113.2–114.0 (LB), 115.3 (RB), 115.5 (RB), 122.6–123.0 (LB), 145.7 (RB), 154.3–154.5 (RB), 159.4 (LB), 166.6 (LB), 167.5–167.7 (LB), 199.3 (RB), and 229.0 (RB). OSM 17708, 17712 (2), 17722, 17726, 17746, and 17750 (2); FMNH 156979 (5), 156981 (2), 156984 (4), and 156989 (4).

Old Shell Records (1966 Survey).—River mile 15.0, 129.8, 156.0, 184.5, and 196.3–198.1. OSM 18211, 18319, 18371, 18387, and 18446.

Leptodea leptodon (Rafinesque, 1820)

Leptodea leptodon (Rafinesque):
Parmalee (1967:92)
Lampsilis leptodon Rafinesque (=*tenuissima* Lea):
Baker (1906:69)

Baker (1906:69) reported that Ferriss collected this species in the Illinois River. No other record of *leptodon* from the Illinois was located. Van der Schalie (pers. comm., 31 August 1967) believed it doubtful that this mussel ever occurred in the Illinois. Parmalee (1967: 92) listed *leptodon* as a species of doubtful occurrence in Illinois, and he made no mention of its ever having lived in the Illinois River. According to Stansbery (pers. comm., 31 July 1968):

> "Recent collection records show this species to exist in relic populations in Oklahoma, Arkansas, Missouri, and Kentucky. It may be extirpated from the rest of its former range. Despite its extensive former range, its former presence in the Illinois River (substantiated only by a single literature record unsupported by a museum specimen) is doubtful."

The author was of the opinion that the above record of *leptodon* being taken from the Illinois River should be considered as doubtful.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Pink Heel-Splitter
Proptera alata (Say, 1817)
(Plate 2-10)

Proptera alata (Say):
    Parmalee (1967:81; 1962:9)
    Richardson (1928:457)
    FMNH
    MCZ
Lampsilis alatus Say:
    Kelly (1899:401)
Lampsilis alata Say:
    Baker (1906:68)
    Forbes & Richardson (1913:529)
Lampsilis alata (Say):
    Danglade (1914:10)
Potamilus alata megapterus Rafinesque, 1820:
    Morrison (pers. comm., 4 January 1968)
Potamilus alatus:
    OSM

The extreme upstream records from the Illinois River of this species known to the author were a single specimen taken in the La Salle-Peru section by Forbes & Richardson (1913:529–530) in 1912 and the pre-1910 MCZ collections. Danglade (1914:37 & 44) considered *alata* fairly common, and he reported taking it at most of his principal stations between Henry and Grafton. In the 1896-1897 period Kelly (1899:401) examined 38 specimens collected in the vicinity of Havana.

Richardson (1928:456–457) reported that by the mid-1920's pollution had eliminated the pink heel-splitter from the river above the Peoria Narrows.

Of this species, 16 live specimens were taken from the Illinois River in the 1966 survey between river miles 1.0 and 196.1 (at Henry). The pink heel-splitter ranked 13th in abundance (Tables 6 and 7). The shell age determinations indicated that these specimens ranged from 9 to 17 years. This mussel had no value as a commercial shell in 1966. The presence of the pink heel-splitter in the Peoria-Pekin area indicated that this species was one of the more tolerant mussels to pollution; this mussel had extended its range upstream since the mid-1920's from the Peoria Narrows to Henry. However, it evidently was unable to tolerate existing pollution conditions upstream as far as the La Salle-Peru area where it had been taken in 1912 by Forbes & Richardson.

The decrease in the abundance of this species in the river since 1912 apparently was caused by pollution.

The host fish for the pink heel-splitter is not known.

Museum Records.—Peru (pre-1910) MCZ; Peoria Narrows (1925) INHS J-1; Havana (1895 Hay) FMNH 6500, (pre-1900 Strode) UIMNH 15175, and (1912 Danglade) USNM 678615; Meredosia (1955 Parmalee) ISM 1382–1384; Naples (1955 Parmalee) ISM 1119–1121; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678577 and (1907 Bartsch stat. 109) USNM 678578; Calhoun County (1928 Baker) UIMNH 27295; and Illinois River without locality (pre-1900) OSM 14593.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 13.0 (RB), 13.2–13.5 (LB), 47.5 (LB), 53.8 (LB), 57.6 (RB), 60.8 (RB), 75.8 (RB), 154.4–

154.5 (RB), 159.7–160.0 (RB), 161.2 (RB), and 196.1 (LB). OSM 17694 and 17744; FMNH 156962–156964, 156978, 156995, and 156996.

Old Shell Records (1966 Survey).—River mile 15.0, 66.0–66.4, 75.8, Quiver Lake, and 184.5. OSM 18212, 18225, 18258, 18307, and 18385.

Fat Pocketbook

Proptera capax (Green, 1832)

Proptera capax (Green):
  Parmalee (1967:83)
Unio capax Green:
  Calkins (1874:41)
Lampsilis capax (Green):
  Danglade (1914:10)
Potamilus capax:
  OSM

Relative to the fat pocketbook, Danglade (1914:46) wrote:

> "This is a rare species in the Illinois, and was found more frequently below locks and dams where the water was swifter."

Danglade (1914:37) did not take this species in 1912 between Henry and Peoria Lake; however, he did collect it at eleven of his principal stations between Pekin and Grafton. Calkins (1874:41–42) reported taking *capax* in La Salle County (Starved Rock pool) in the early 1870's. One museum specimen of this species from the river was examined by the author and another was checked by Dr. Stansbery (pers. comm., 22 December 1969).

This species probably disappeared from the upper river by 1900 and from the middle and lower river before 1920.

The fish host for this mussel is not known.

Museum Records.—Illinois River without locality INHS and (pre-1900) OSM 4474.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Fragile Heel-Splitter

Proptera laevissima (Lea, 1829)
(Plate 2-9)

Leptodea laevissima (Lea):
  Parmalee (1967:74)
  Richardson (1928:457)
Lampsilis laevissimus Lea:
  Kelly (1899:401)
Lampsilis laevissima Lea (= *ohioensis* Say):
  Baker (1906:68)
  Forbes & Richardson (1913: 525 & 533)
Proptera laevissima (Lea):
  FMNH
Lampsilis laevissima (Lea):
  Danglade (1914:10)
Potamilus ohiensis Rafinesque, 1820:
  Morrison (pers. comm., 4 January 1968)

Baker (1906:68) reported that the fragile heel-splitter was collected from the river at Utica and at other locations downstream. Danglade (1914:37 & 44) considered this mussel fairly common in the Illinois River, and he reported taking it upstream as far as Peoria Lake in 1912. In that same year Forbes & Richardson (1913:525, 533, & 536) took this species at Ottawa (Starved Rock pool) near the mouth of the Fox River and in the Hennepin-Chillicothe section. By the mid-1920's pollution had eliminated the fragile heel-splitter north of the Narrows at Peoria (Richardson 1928:456–457).

In the 1966 survey this mussel ranked 12th in abundance (Tables 6 and 7); 42 live fragile heel-splitters were taken between river miles 1.0 and 196.1 (Table A-3). These shells ranged from 2 to 13 years in age. The 2-year-old mussels (two specimens) were collected in the Alton pool, and the heights of these specimens were 0.8 inch. The shell of this species was of no commercial value.

Since the fragile heel-splitter was taken in the Peoria-Pekin section, it apparently was one of the mussels more tolerant to pollution; however, it was not collected in the upper part of the Peoria pool. By 1966 the fragile heel-splitter had re-extended its upstream range from the Peoria Narrows (mid-1920's) to Henry (river mile 196.1), a distance of about 29.5 miles. Apparently this species was about as abundant in 1966 as it was before 1913.

The fish hosts known for this mussel are the freshwater drum and the white crappie (Baker 1928:248). These fishes still occur in the Illinois River.

Museum Records.—Thompson Lake FMNH 23218; Quiver Lake (1955 Parmalee) ISM 1034–1035; Havana (1910 Baker) UIMNH 22159; 1 mile W of Havana, backwater slough of the Illinois River (1953 Parmalee) ISM 264–267; Meredosia (1930 Morrison) USNM 678655 and (1955 Parmalee) ISM 1380–1381; Naples (1955 Parmalee) ISM 1109–1111; 1 mile N of Hardin (1956 Parmalee) ISM 2200–2201 (dead); and 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678579.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 13.0 (RB), 42.2–42.3 (LB), 47.5 (LB), 66.0–66.4 (LB), 75.8 (RB), 87.3 (RB), 110.1 (LB), 129.8–130.4 (RB), 145.7 (RB), 154.4–154.5 (RB), 161.2 (LB), 165.3–166.1 (RB), 166.3 (LB), 174.1 (LB), 174.9 (LB), and 196.1 (LB). OSM 17695, 17715, 17727, and 17740; FMNH 156951 (2), 156960 (2), 156974 (2), 156993 (4), and 156994 (2).

Old Shell Records (1966 Survey).—River mile 15.0, 66.0–66.4, 75.8, 83.0, 86.6–86.8, 145.7, 156.0, and 196.3–198.1. OSM 18213, 18224, 18267, 18272, 18335, 18372, and 18447.

Liliput Shell

Carunculina parva (Barnes, 1823)
(Plate 4-23)

Carunculina parva (Barnes):
  Parmalee (1967:59)
  Richardson (1928:457)
  MCZ
Unio parvus Bar.:
  Strode (1891*a*:133)
Lampsilis parvus Bar.:
  Kelly (1899:401)
Lampsilis parva Barnes:
  Baker (1906:67–68)
  Forbes & Richardson (1913:533)
Lampsilis parva (Barnes):
  Danglade (1914:10)
Toxolasma parvum parvum (Barnes):
  FMNH
Toxolasma parva Barnes:
  Morrison (pers. comm., 4 January 1968)

Danglade (1914:45) regarded the liliput shell as a rare species in the Illinois River, and in his survey observed a single specimen taken from Peoria Lake. However, concerning the abundance of this species, Parmalee (1967:59) stated:

> "It has also been observed inhabiting the shallow, mud banks and backwater sloughs of the Illinois River in considerable numbers."

Kelly's (1899:401) data indicated that this shell occurred abundantly in the river in the Havana area in the 1896-1897 period. In 1890 Strode (1891*a*:133) collected the liliput shell in Thompson Lake (now drained and leveed off) near Havana. Forbes & Richardson (1913:533 & 536) took this species in 1912 at Hennepin and in the Henry-Chillicothe section. Dr. William Clench (pers. comm., 12 August 1969) advised the author that a specimen of this species taken from the river at Peru (pre-1910) was in the MCZ collections. By the mid-1920's pollution had restricted the upstream distribution of this species to no farther than Middle Peoria Lake (Richardson 1928:456–457).

In the early 1930's Morrison (pers. comm., 4 January 1968) collected this shell at Meredosia. However, in the 1950's Parmalee (pers. comm., 21 November 1966) did not collect a live liliput shell at Meredosia or at any of his other collecting sites in the river proper athough he did take live specimens of this mussel in 1953 from a backwater slough about 1 mile west of the river and Havana. In the 1966 survey a single live specimen of this species was taken by wading at river mile 1.0. Apparently by 1966 the liliput shell was confined to the extreme lower section of the river proper.

The host fish for this mussel is not known.

Museum Records.—Peru (pre-1910) MCZ; Peoria (1931 Morrison) USNM 678659 (dead); Quiver Lake (1955 Parmalee) ISM 1053 (dead); 1 mile W of Havana in backwater slough (1953 Parmalee) ISM 268; Beardstown (1870) FMNH 14337; Meredosia (Hinkley) UIMNH 4307, (1909 Baker) UIMNH 21361, (1930 Morrison) USNM 678656–678657, and (1932 Morrison) USNM

678658; 1 mile N of Hardin (1956 Parmalee) ISM 2207 (dead); and Illinois River without locality (1870's) BK.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB). OSM 18016.

Old Shell Records (1966 Survey).—River mile 83.0 and Quiver Lake. OSM 18266 and 18308.

Black Sand-Shell

Ligumia recta (Lamarck, 1819)

Ligumia recta (Lamarck):
  Parmalee (1967:74; 1962:9)
Unio rectus Lam.:
  Calkins (1874:44)
Lampsilis rectus Lam.:
  Kelly (1899:401)
Lampsilis recta Lamarck:
  Baker (1906:66)
Lampsilis recta (Lam.):
  Danglade (1914:10)
Ligumia recta latissima Rafinesque, 1820:
  Morrison (pers. comm., 4 January 1968)
Ligumia latissima Raf.:
  MCZ

In the early 1870's Calkins (1874:44) found the black sand-shell occurring abundantly in the upper Illinois River (Starved Rock pool), and he remarked that the shells here attained a length of 6–7 inches. In the 1896-1897 period Kelly (1899:401) examined 10 specimens of this species collected in the vicinity of Havana. Danglade (1914:37 & 45) considered this shell rather common in 1912; however, he did not take it north of Chillicothe. Forbes & Richardson (1913) and Richardson (1928) did not record this species from the upper and middle river between 1912 and 1925.

The black sand-shell was not taken alive from the Illinois River in the 1966 survey. Neither Morrison (pers. comm., 4 January 1968) in the early 1930's nor Parmalee (pers. comm., 21 November 1966) in the 1950's collected a live specimen of this species from the river.

The museum and old shell records indicated that the black sand-shell formerly was distributed throughout most of the Illinois River. Apparently by 1912 pollution had eliminated this shell above Chillicothe and by 1930 from the entire river.

The host fish for this mussel is not known.

Museum Records.—La Salle County (Baker) UIMNH 15134; Peoria (1870's) BK; Havana (1912) INHS a-78; Meredosia (1907 Freeland) USNM 676953 and (pre-1910) MCZ; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678580; Calhoun County (1928 Baker) UIMNH 27296; Illinois River stat. K_2 (1907 Freeland & Williams) USNM 676964; and Illinois River without locality (1870's) BK.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 75.8, 129.8, 145.7, 156.0, 240.4, and 253.5–256.5. OSM 18259, 18320, 18336, 18373, 18469, and 18483.

Pond Mussel

Ligumia subrostrata (Say, 1831)

Ligumia subrostrata (Say):
  Parmalee (1967:75)
Lampsilis subrostrata Say (= *mississippiensis* Conrad):
  Baker (1906:67)

Baker (1906:67) reported that Derr collected this shell at Peru in La Salle County; however, the name of the stream was not mentioned. Morrison (pers. comm., 27 November 1967) was of the opinion that this specimen undoubtedly was taken in a tributary stream rather than in the Illinois River.

In 1954 Parmalee (pers. comm., 21 November 1966) collected a pond mussel in a mud slough backwater 1 mile west of Havana and the Illinois River.

The author was of the opinion that these records of *subrostrata* should be considered as records from the Illinois River valley rather than from the Illinois River and its adjoining bottomland lakes.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Rainbow-Shell
Villosa iris iris (Lea, 1829)

Villosa (= *Micromya*) *iris* (Lea):
Parmalee (1967:75–76)
Unio iris Lea:
Calkins (1874:42)

Calkins (1874:42) reported that this species was not abundant in the Illinois River at La Salle County (Starved Rock pool) in the early 1870's. No museum specimen of the rainbow-shell was located from the Illinois River. Morrison (pers. comm., 14 June 1968) informed the author that the collections of the U.S. National Museum contained a specimen (USNM 58260) of this species taken by Calkins from the Vermilion River (a tributary stream of the Illinois) in La Salle County. It was apparent from this record that Calkins was quite familiar with the rainbow-shell, and no doubt he identified it properly as *U. iris* in his Illinois River collections.

According to Parmalee (1967:76), this species still occurs in the Kankakee, Fox, and Vermilion rivers, tributary streams of the upper Illinois River. The Fox and Vermilion rivers empty into the Illinois near the vicinity where Calkins made his collections.

Relative to the ecology of this species, *Ligumia iris novieboraci* (Lea), Baker (1928:262) stated that it is:

> "A mussel of small streams, living below riffles on a sandy or mud bottom. Also in riffles on a gravel bottom in less than a meter of water."

In the Starved Rock area where Calkins (1874:11) collected, the river was shallow and the bottom sandy. Evidently this habitat was suitable for the support of a small population of rainbow-shells when Calkins (1874:42) made his collections, and his record of its occurrence there, in the author's opinion, was authentic. Later this excellent mussel habitat was destroyed by pollution, siltation, and the Starved Rock dam.

The fish host for this mussel is not known.

Museum Records.—None.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Yellow Sand-Shell
Lampsilis anodontoides forma anodontoides (Lea, 1831)

Lampsilis anodontoides (Lea):
Parmalee (1967:64)
Forbes & Richardson (1913:536)
Danglade (1914:10)
Richardson (1928:457)
Unio anodontoides Lea:
Calkins (1874:41)
Strode (1891*a*:133)
Lampsilis anodontoides Lea:
Kelly (1899:401)
Lampsilis anodontoides Lea (= *teres* Say):
Baker (1906:66)
Lampsilis (Ligumia) teres teres (Raf.):
FMNH
Lampsilis teres Rafinesque, 1820:
Morrison (pers. comm., 4 January 1968; 4 June 1968)

Before 1899 *L. anodontoides* f. *anodontoides* was not separated from *L. anodontoides* f. *fallaciosa* (Smith 1899); consequently, the early published records of the occurrence of the yellow sand-shell in the Illinois River by Calkins (1874:41), Strode (1891*a*:133), and Kelly (1899:401) may have referred to either or both forms of *anodontoides*. In the case of Calkins' record of *anodontoides*, Morrison (pers. comm., 4 June 1968) wrote:

> "In W. W. Calkins, Proc. Ottawa Acad. Sci., 1874, list of La Salle County, there is the listing of *Unio anodontoides* from the Illinois River. We have 5 specimens from W. W. Calkins (from the Stearns Collection) from the Illinois River, probably representing this record. These shells, catalogued February 2, 1886, as USNM 40773, were labeled *anodontoides*. Actually, only the three largest shells of this lot are *teres (anodontoides)* as we know it today. The two smaller ones are *fallaciosa*,

> so Calkins' record from La Salle County also included *fallaciosa* from this stretch of the Illinois River. F. C. Baker's record of '*L. anodontoides*' (Moll. Chicago Area, I, p. 100, 1898) corroborates the occurrence of *fallaciosa* farther upstream in the Illinois system and/or northward than *teres*. Baker's description, p. 100, of the beak sculpture and the figures of his shells, especially the smaller, lower figures, prove that he recorded only *Lampsilis fallaciosa* (which was named only a few months later) from the Des Plaines River and its tributaries only. In the 1906 Catalogue of Illinois Shells, Baker put this Cook County record under *fallaciosa* (p. 66) and listed *teres* only as La Salle County (Huett) and 'Northern Illinois' (Calkins). Since Baker did not have access to our USNM 40773 specimens, he did not know that Calkins had both *teres* and *fallaciosa* in the La Salle County, Illinois River collections, collected alive earlier and published in 1874. The *fallaciosa* of Calkins are now recatalogued as USNM 679106."

Concerning the yellow sand-shell in the Illinois River in 1912, Danglade (1914: 45) stated:

> "This species is found sparingly throughout the upper river, but is fairly abundant in the Hardin district, where it is in sufficient quantity to be sorted out and sold separately at an advanced price. This shell is the most valuable of the fresh-water mussels . . . . It prefers deep water and clean sandy bottoms."

Danglade (1914:37) did not collect this shell above Peoria Lake; however, Forbes & Richardson (1913:536) took it in 1912 in the Henry-Chillicothe section of the river. In the mid-1920's Richardson (1928:456–457) failed to collect the yellow sand-shell in his survey of Peoria Lake.

In 1930 Morrison (pers. comm., 4 January 1968) took this mussel alive at Meredosia. Parmalee (pers. comm., 21 November 1966) did not take it at Meredosia in 1955 but did collect a live specimen downstream at Naples.

No live yellow sand-shell was taken in the 1966 survey. Of the mussel species tested by Ellis (1936:39), the yellow sand-shell *(L. teres)* was the most readily killed by silt deposits. Evidently siltation and pollution adversely affected this mussel in the Illinois River.

The fish host for the yellow sand-shell is the longnose gar, *Lepisosteus osseus* (Linnaeus), and other possible fish hosts are the shortnose gar, *Lepisosteus platostomus* Rafinesque; alligator gar, *Lepisosteus spatula* Lacépède; green sunfish; orangespotted sunfish, *Lepomis humilis* (Girard); largemouth bass; white crappie; and black crappie (Baker 1928:267). All of these fishes, except the alligator gar, still occur in the Illinois River.

Museum Records.—La Salle County (1870's Calkins) USNM 40773; Havana (1895 Hay) FMNH 6392 and (pre-1900 Strode) FMNH 9123; Frederick (Wettengel) FMNH 68411; Meredosia (1912 Danglade) USNM 678616 and (1930 Morrison) USNM 678660; Naples (1955 Parmalee) ISM 928 (dead) and 1158; Buckhorn Landing (1912 Danglade) USNM 678617; and 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678581.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 167.2. OSM 18379.

Slough Sand-Shell
Lampsilis anodontoides
forma fallaciosa (Smith, 1899)
(Plate 3-16)

Lampsilis fallaciosa Rafinesque [sic]:
 Parmalee (1967:65; 1962:9)
Unio anodontoides Lea:
 Calkins (1874:41)
Lampsilis fallaciosa (Smith) Simpson:
 Baker (1906:66)
 Forbes & Richardson (1913:533)
 Richardson (1928:457)
Lampsilis fallaciosa (Smith):
 Danglade (1914:10)
Lampsilis fallaciosa Smith, 1898:
 Morrison (pers. comm., 4 January 1968; 4 June 1968)

Lampsilis anodontoides Lea:
MCZ
Lampsilis (Ligumia) teres fallaciosa (Simpson):
FMNH

Danglade (1914:37 & 45) reported that the slough sand-shell occurred abundantly in the Illinois River in 1912 and that he collected it at all of his principal stations between Henry and Grafton. Concerning the ecology of this mussel in the river, Danglade (1914:45) stated that it is:

> "usually found standing on end burrowed in the mud of sloughs and bays or along the shore where there is but little current."

These habits of the slough sand-shell made it difficult for us to catch it with the crowfoot bar and dredge in the 1966 survey. In the survey 53 live specimens of this shell were collected (Table A-3) of which 66.0 percent were taken by wading. This shell ranked ninth in abundance; however, it probably occurred more abundantly than was reflected by our collections (Tables 6 and 7). The author believed that if more wading collections had been made in the survey this mussel probably would have ranked about sixth in abundance rather than ninth. The mean height of the slough sand-shell was 1.5 inches (range 1.0–2.0 inches), and the ages of the shells ranged from 3 to 12 years. The shell of this species was of no commercial value.

The *Lampsilis anodontoides* shells from the Illinois River in the Museum of Comparative Zoology were checked for the author by Dr. Stansbery (pers. comm., 20 January 1970) and he determined them to be form *fallaciosa*.

Calkins (1874:41) collected this shell in the early 1870's as discussed above under *L. anodontoides* f. *anodontoides*, in the river at La Salle County (Starved Rock pool). In the 1966 survey two live slough sand-shells were taken at about river mile 226.1 (at La Salle), only about 5 miles below Starved Rock where Calkins (1874:11) did much of his collecting in the river. The slough sand-shell was collected about 18.5 miles farther upstream in 1966 than it was in 1912 by Forbes & Richardson (1913:533). In the mid-1920's Richardson (1928:457) did not take this shell above the lower end of Upper Peoria Lake. Apparently the slough sand-shell was one of the more tolerant species of mussels to pollution in the Illinois.

The white crappie, shortnose gar, and the shovelnose sturgeon, *Scaphirhynchus platorynchus* (Rafinesque), are believed to be the host fishes for the slough sand-shell (Baker 1928:269). The shovelnose sturgeon is now extremely rare in the Illinois River.

Museum Records.—La Salle County (1870's Calkins) USNM 679106; Peru (pre-1910) MCZ 70918; Spring Valley, "Sandy River Drift" (1924 Morrison) USNM 678668 (dead); Mossville (1925) INHS C-5; Peoria Narrows (1924) INHS 1-B; Peoria, above bridge (1912 Danglade) USNM 678618; Peoria (1870's) BK, (1931 Morrison) USNM 678661 and 678663, and (pre-1910) MCZ 29925; between Pekin and Havana USNM 677042; Liverpool (1957 Parmalee) ISM 2370–2377; Quiver Lake (1955 Parmalee) ISM 996–1001; Havana (1894 Baker) UIMNH 22151, (1909 Freeland) USNM 678619, (1912 Danglade) USNM 678620, and (1912) INHS a-22-S; Frederick (pre-1917 Zetek) FMNH 67968; 2 miles N of Beardstown (1959 Parmalee) ISM 2869–2870; Beardstown (1910) INHS F-92; Meredosia (1930 Morrison) USNM 678662, (1932 Morrison) USNM 678664, and (1955 Parmalee) ISM 1415–1418; Naples (1955 Parmalee) ISM 1159–1164; 1 mile N of Hardin (1956 Parmalee) ISM 2204–2205 (dead); 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678582 and (1907 Bartsch stat. 109) USNM 678583; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678584; and Illinois River without locality (1907 Freeland & Williams) FMNH 11231.

Live Mussel Records (1966 Survey).—River mile 1.0 (LB), 13.0 (RB), 47.5 (LB), 56.3 (LB), 57.6 (RB), 58.9 (RB), 66.0–66.4 (LB), 73.7 (RB), 75.8 (RB), 86.8 (LB), 87.3 (RB), 87.9 (LB), 95.8 (LB), 100.0–100.5 (LB), 129.8–130.4

(RB), 163.0 (LB), 164.5–165.3 (LB), 166.3 (LB), 167.7 (LB), 169.5 (LB), 174.1–174.9 (RB), 174.1 (LB), 174.9 (LB), 184.5 (RB), 196.1 (LB), 198.1 (RB), 224.0 (LB), and 225.8–226.1 (RB). OSM 17347 (3), 17696, 17718, 17721, 17734, 17741, 17745, and 17748; FMNH 156980 (2), 157001 (2), and 157007 (10).

Old Shell Records (1966 Survey).—River mile 15.0, 44.9, 66.0–66.4, 75.8, 83.0, 86.6–86.8, 106.8, Quiver Lake, 129.8, 145.7, 156.0, 184.5, 196.1, and 196.3–198.1. OSM 18206, 18214, 18260, 18268, 18273, 18297, 18309, 18337, 18374, 18386, and 18435.

Fat Mucket
Lampsilis radiata luteola
(Lamarck, 1819)
(Plate 3-17)

Lampsilis siliquoidea (Barnes):
Parmalee (1967:68; 1962:9)
Richardson (1928:457)
MCZ
Unio luteolus Lam.:
Calkins (1874:42–43)
Lampsilis luteolus Lam.:
Kelly (1899:401)
Lampsilis luteola Lamarck (=*siliquoides* Barnes, *distans* Anthony):
Baker (1906:65)
Lampsilis luteola (Lam.):
Danglade (1914:10)
Forbes & Richardson (1913:533)
Lampsilis luteola Lamarck, 1819:
Morrison (pers. comm., 4 January 1968)
Lampsilis (Ligumia) siliquoidea siliquoidea (Barnes):
FMNH

In the early 1870's Calkins (1874:42–43) found the fat mucket occurring abundantly in the Illinois River at La Salle County (Starved Rock pool). Kelly (1899:401) examined 11 specimens collected in the Havana area in the 1896-1897 period. Danglade (1914:46) considered the fat mucket widely distributed in the Illinois and found that it was more plentiful in Peoria Lake than elsewhere. In 1912 Danglade (1914:37) took this mucket at all of his principal stations between Henry and Beardstown but collected it only intermittently at his stations between Beardstown and Grafton.

In the 1966 survey of the Illinois River only eight live fat muckets were collected (Table A-3). Stansbery (pers. comm., 26 September 1967) referred to these specimens as *Lampsilis radiata siliquoidea* (Barnes, 1823) based on the intergrading of *radiata* and *siliquoidea* discovered by Clarke and Berg (1959: 58–62). Later, Stansbery (pers. comm., 14 August 1969) advised the author to refer to the Illinois River material as *Lampsilis radiata luteola* (Lam., 1819).

The fat mucket ranked 16th in abundance in the 1966 survey (Tables 6 and 7) and the ages of the specimens collected ranged from 11 to 20 years.

Live fat muckets were collected in 1966 between river miles 110.5 (below Havana) and 169.3 (Peoria Lake). Six of the eight fat muckets came from Peoria Lake, where in 1912 Danglade (1914:46) also found this mussel occurring in its greatest abundance. In 1912 Forbes & Richardson (1913:533) collected the fat mucket upstream as far as Hennepin. In the mid-1920's Richardson (1928:456–457) found that pollution had limited the upstream distribution of this mussel to the lower end of Upper Peoria Lake, only about 3 miles above its farthest upstream location in the 1966 survey. In the Alton pool, Morrison (pers. comm., 4 January 1968) collected this mussel at Meredosia in 1930, and in 1955 Parmalee (pers. comm., 21 November 1966) collected it at Meredosia and Naples. As indicated above, the fat mucket was not taken alive in the Alton pool in the 1966 survey; however, a single specimen of this mussel was observed in a culled commercial shell pile at Meredosia. The present scarcity and limited range of this once abundant mussel together with the lack of any young breeding stock portended its possible elimination from the Illinois River.

The bluegill, yellow perch, and walleye, *Stizostedion vitreum vitreum* (Mitchill), are the known natural host fishes for the fat mucket (Baker 1928: 273), but the walleye is uncommon in the Illinois River.

Museum Records. — La Salle (pre-1910) MCZ; Peru (pre-1910) MCZ; Havana (1894 Baker) UIMNH 22145, (1895 Hay) FMNH 14074, (1910 Zetek) FMNH 59306 and 68163, and (1912 Danglade) USNM 678621; Meredosia (1930 Morrison) USNM 678665, (pre-1910) MCZ, and (1955 Parmalee) ISM 1413–1414; Naples (1955 Parmalee) ISM 1165–1169; and 1 mile below Hardin (1907 Bartsch stat. 109) USNM 678585.

Live Mussel Records (1966 Survey).— River mile 110.5 (RB), 122.2 Quiver Lake (LB), 166.6 (LB), 167.7 (LB), 168.2 (RB), and 169.3 (RB). OSM 17725, 17730 (2), 17733, and 17739; FMNH 156997. (1969): River mile 162.3 (LB). OSM 22277.

Old Shell Records (1966 Survey).— River mile 66.0–66.4, 75.8, 106.8, Quiver Lake, 145.7, 156.0, 167.2, 184.5, and 196.3–198.1. OSM 18158, 18226, 18261, 18298, 18338, 18375, 18380, and 18448.

Pocketbook

Lampsilis ventricosa (Barnes, 1823)

Lampsilis ventricosa (Barnes):
  Parmalee (1967:70; 1962:9)
  Forbes & Richardson (1913:525 & 533)
  Richardson (1928:457)
  Danglade (1914:10)
  MCZ
Lampsilis ventricosus Bar.:
  Kelly (1899:401)
Lampsilis ventricosa Barnes (= *occidens* Lea, *subovata* Lea):
  Baker (1906:64)
Lampsilis (Lampsilis) cardium (Raf.):
  FMNH
Lampsilis occidens:
  Richardson (1928:457)
Lampsilis cardium Rafinesque, 1820:
  Morrison (pers. comm., 4 January 1968)

No live pocketbook was taken in the 1966 survey of the Illinois River. Neither Morrison (pers. comm., 4 January 1968) in the early 1930's nor Parmalee (pers. comm., 21 November 1966) in the 1950's collected a live pocketbook from the Illinois.

Cvancara (1963:223) recognized the possibility that a cline may exist in the *Lampsilis ovata* complex; however, he mentioned that considerable study remained to be done on the anatomy and genetics of the three species involved in this complex. Morrison (pers. comm., 4 January 1968) referred to the Illinois River specimens of this mussel in the U. S. National Museum collections as *L. cardium* Rafinesque, 1820, and Stansbery (pers. comm., 13 January 1968) identified the two old shells collected in the 1966 survey as *L. ovata* forma *ventricosa* (Barnes, 1823). Since no special study was made of the limited number of Illinois River museum specimens available, the author decided to refer to them here merely as *L. ventricosa,* the usual reference to the northern form (Cvancara 1963:222).

This species was not taken in the upper river by Calkins (1874). In 1912 a live pocketbook was collected by Forbes & Richardson (1913:525) in the Illinois River at Ottawa near the mouth of the Fox River. In that same year they (1913:533) took two dead shells of this species at Hennepin. Danglade (1914:37) did not collect this species in the Henry-Chillicothe section of the river, but he did take it at most of his principal stations between Peoria Lake and Grafton. In the 1896-1897 period Kelly (1899:401) examined 10 specimens of this mussel from the Havana area.

In 1912 Danglade (1914:46) considered the pocketbook an uncommon mussel in the Illinois. By the mid-1920's this species had disappeared from Peoria Lake (Richardson 1928:457). According to Parmalee (1967:70): "The Pocketbook thrives on a sand or gravel bottom, in current at depths of less than one foot to over 10 feet." Siltation and pollution probably eliminated this mussel from the Illinois River between 1918 and 1930.

The natural host fishes for the pocketbook are the white crappie and the sauger (Baker 1928:284).

Museum Records.—Peru (pre-1910) MCZ; between Pekin and Havana (1907 Freeland & Williams) USNM 677059; Havana (1894 Baker) UIMNH 22154; Meredosia (1907) USNM 676952; Florence (1909 Freeland) USNM 678622; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678586; 10 miles below Hardin (1907 Bartsch stat. 110) USNM 678587; and Illinois River without locality (1895 Hay) FMNH 14070, (pre-1943 Webb Coll.) FMNH 23307, and (1870's) BK.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 145.7 and 219.4. OSM 18339 and 18466.

Lampsilis orbiculata Complex

Whether *Lampsilis orbiculata* and *L. higginsi(i)* are separate species remains an open question (Stansbery, pers. comm., 26 September 1967; van der Schalie, pers. comm., 19 January 1968). Morrison (pers. comm., 27 November 1967) recognizes *L. abruptus* Say, 1831 ("*orbiculatus* auct, NON Hild.") and *L. higginsi* Lea, 1868 as two separate species. Stansbery (pers. comm., 26 September 1967) considers that:

> "*Lampsilis orbiculata* and *Lampsilis higginsii* are distinguishable but I have not enough specimens (nor have I seen enough material in other museums) to enable me to infer whether or not they are conspecific. This being the case, I carry them simply as forms of the same nominal species. I will not be surprised if they are found to be conspecific nor would I be surprised to find they are different species. I just don't know at present."

Since this is an unsettled problem needing further study, the author has followed Stansbery's and van der Schaile's opinions and has treated the Illinois River material as forms of *Lampsilis orbiculata*.

No live specimen belonging to this complex was taken in the 1966 survey of the river. As a result, the author has depended upon old shells taken in the 1966 survey, literature records, and museum records to establish the former occurrence of this complex in the Illinois River. Since the identification of the two forms, or species, involved here is quite difficult, the question is raised as to the validity of the Illinois River records of the two species or forms of this complex in the literature and of the identifications made years ago of museum specimens. The museum specimens of this complex from the Illinois River that have not been checked recently are listed as *L. orbiculata* complex. This list also includes the specimens examined by the author and one old shell taken in the 1966 survey and checked by Dr. Stansbery. Other Illinois River specimens belonging to this complex and deposited in various collections were checked by the following persons: Benjamin Koons' specimens, Illinois Natural History Survey specimens, and U. S. National Museum collections by Dr. Morrison; subfossil shells taken in the 1966 survey by Dr. Stansbery; and the Illinois State Museum collection by Dr. Parmalee. The author has used the identifications made by these taxonomists as the basis for his discussion of the two forms or species of this complex under the next headings of *L. orbiculata* forma *orbiculata* and *L. orbiculata* forma *higginsii*.

Museum Records. — (*L. orbiculata* complex) Starved Rock (Hinkley) UIMNH 4117; La Salle County (Daniels) UMMZ 86345; Havana (1894 Baker) UIMNH 22153 and (Smith) UMMZ 84351; and Illinois River without locality (1861 Hall) FMNH 14233.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—River mile 253.5. OSM 18484.

Lampsilis orbiculata
forma orbiculata (Hildreth, 1820)

Lampsilis orbiculata (Hildreth):
    Parmalee (1967:67)
    Danglade (1914:10)
Lampsilis orbiculata Hildreth:
    Baker (1906:66)
Lampsilis abruptus Say, 1831:
    Morrison (pers. comm., 4 January 1968)

According to Baker (1906:66) this form or species was collected from the

Illinois River by Strode. Concerning *orbiculata,* Danglade (1914:46) stated:

> "There are two examples in our collection, one from Chillicothe and the other from Peoria. The nacre of one is rather pinkish. This species is difficult to separate from *higginsii,* but is generally more southern in distribution."

Morrison (pers. comm., 4 January 1968) examined two specimens in the collections of the U. S. National Museum taken from the Illinois River 1 mile below Hardin in 1907. He identified them as *L. abruptus* and *L. higginsi.* This was of particular interest in that both of these species or forms had been found occurring together in the river. Morrison (pers. comm., 27 November 1967) commented that: "The geographic range of *abruptus* overlaps that of *higginsi* in the region of the Ohio-Mississippi confluence."

The only record recognized by the author of the occurrence of *L. orbiculata* f. *orbiculata* (*abruptus*) in the Illinois was the one mentioned above from the lower river furnished by Dr. Morrison. It appeared to the author that this form or species was never common in the Illinois and occurred only in the lower part of the river. The literature citations given above for the occurrence of *L. orbiculata* f. *orbiculata* may refer to either or both of the forms or species of the *L. orbiculata* complex. This mussel had probably disappeared from the Illinois River before 1930.

The fish host of *L. orbiculata* f. *orbiculata* is not known.

Museum Records.—1 mile below Hardin (1907 Bartsch stat. 108) USNM 678666.

Live Mussel Records (1966 Survey).—None.

Old Shell Records (1966 Survey).—None.

Higgin's Eye
Lampsilis orbiculata
forma **higginsii** (Lea, 1857)

Lampsilis higginsii (Lea):
  Parmalee (1967:67)
  Danglade (1914:10)
  Baker (1928:294)
Unio orbiculatus Hildreth:
  Calkins (1874:44)
Lampsilis higginsii Lea:
  Kelly (1899:401)
  Baker (1906:66)
Lampsilis higginsii var. *grandis* Simpson, 1914:
  Simpson (1914:79)
Lampsilis higginsi Lea, 1868:
  Morrison (pers. comm., 4 January 1968)

Calkins (1874:44) found *U. orbiculatus* occurring abundantly in the Illinois River at La Salle County (Starved Rock pool) in the early 1870's. Morrison (pers. comm., 4 January 1968) identified a specimen collected by Calkins from the river as *L. higginsi.* This record and Simpson's (1914:79) report of finding *L. higginsii* var. *grandis* occurring fairly abundantly in the river near Utica—in the vicinity where Calkins (1874:11) collected *U. orbiculatus* —led the author to believe that Calkins took *L. orbiculata* f. *higginsii* rather than *L. orbiculata* f. *orbiculata* from the river in La Salle County.

The author submitted four specimens of the *L. orbiculata* complex from the Benjamin Koons collection and the collection of the Illinois Natural History Survey to Dr. Morrison for identification. Morrison (pers. comm., 4 January 1968) stated that:

> "The four specimens sent for check are indeed *Lampsilis higginsi* Lea. The large female with the more widely produced post basal region is the form called *Lampsilis higginsi grandis* by Simpson (1914:79). Without a great many more specimens available for study, I would not use the *grandis* form name."

Two of these specimens were collected from the river at Havana in 1895 and 1912. Kelly (1899:401) reported that he examined a single specimen of *L. higginsii* in the 1896-1897 period from the Havana area of the river.

A subfossil shell collected in the 1966 survey at river mile 94.3 (below Browning) was identified by Stansbery (pers. comm., 13 January 1968) as *Lampsilis orbiculata* f. *higginsii.* Parmalee (pers. comm., 29 June 1967) indicated that the Illinois State Museum contained two specimens of *L. higginsii* collected in the 1870's at Peoria.

Danglade (1914:37) reported taking

higginsii at Chillicothe, Peoria Lake, Havana, Bath, Beardstown, Meredosia, Florence, Pearl, Kampsville, Hardin, and Twelve-Mile Island. He (1914:46) considered *higginsii* as uncommon but widely distributed, especially in the lower half of the river. Neither Forbes & Richardson (1913) in 1912 nor Richardson (1928) in the mid-1920's reported taking a mussel belonging to the *L. orbiculata* complex above Peoria. Apparently *higginsii* formerly was widely distributed in the Illinois River before 1900 and gradually was eliminated by pollution and siltation before 1930.

The known host fish for *higginsii* is the sauger (Baker 1928:294). As mentioned earlier, this is an uncommon fish in the Illinois River.

Museum Records. — Peoria (1870's) ISM 769–770; Havana (1895) INHS and (1912) OSM 23250; 1 mile below Hardin (1907 Bartsch stat. 108) USNM 678588; and Illinois River without locality (Calkins) USNM 58129 and (1870's) OSM 23249.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— River mile 94.3. OSM 18287.

Snuffbox

Dysnomia triquetra (Rafinesque, 1820)

Dysnomia triquetra (Rafinesque):
Parmalee (1967:62)

Unio triangularis Barnes:
Calkins (1874:45)

Truncilla triquetra Rafinesque (= *triangularis* Lea):
Baker (1906:63)

The snuffbox was taken by Calkins (1874:45) in the Illinois River in La Salle County (Starved Rock pool) in the early 1870's. According to Baker (1906:63), this species was collected from the river by Handwerk. The author examined a shell (UIMNH 15257) of this species collected by Baker at La Salle; however, the name of the stream was not recorded. Possibly this shell came from the Illinois. Another shell of this species, examined by the author, was collected by Baker in 1911 from the Illinois River in Fulton County. The snuffbox was not taken from the river by Danglade (1914). Evidently this species was never common in the Illinois and was probably quite scarce by 1911.

The fish host of the snuffbox is not known.

Museum Records. — Fulton County (1911 Baker) UIMNH 3766.

Live Mussel Records (1966 Survey).— None.

Old Shell Records (1966 Survey).— None.

EFFECTS OF POLLUTION

In the preceding section it has been established that at least 49 different kinds of mussels were present in the Illinois River and its adjoining bottomland lakes in the 1870-1900 period (Table 5). Apparently between the 1870-1900 and 1906-1912 periods[1] three typical small stream species of mussels (*A. calceolus, A. marginata,* and *V. iris iris*) were ex-

Table 9.—Kinds of mussels extirpated from the Illinois River and its bottomland lakes between 1900 and 1969.[a]

Cumberlandia monodonta (Spectacle-Case)

Fusconaia flava f. *flava* (Wabash Pig-Toe)

Quadrula metanevra (Monkey-Face)

Cyclonaias tuberculata (Purple Warty-Back)

Plethobasus cyphyus (Bullhead)

Pleurobema coccineum f. *solida*

Pleurobema pyramidatum

Elliptio crassidens (Elephant's Ear)

Elliptio dilatatus (Lady-Finger)

Uniomerus tetralasmus (Pond-Horn)[b]

Lasmigona costata (Fluted Shell)

Alasmidonta calceolus (Slipper-Shell)

Alasmidonta marginata (Elk-Toe)

Strophitus undulatus (Squaw Foot)

Anodontoides ferussacianus (Cylindrical Paper Shell)

Actinonaias ligamentina (Mucket)

Plagiola lineolata (Butterfly)

Proptera capax (Fat Pocketbook)

Ligumia recta (Black Sand-Shell)

Villosa iris iris (Rainbow-Shell)

Lampsilis anodontoides f. *anodontoides* (Yellow Sand-Shell)

Lampsilis ventricosa (Pocketbook)

Lampsilis orbiculata f. *orbiculata*

Lampsilis orbiculata f. *higginsii* (Higgin's Eye)

Dysnomia triquetra (Snuffbox)

[a] *Anodonta suborbiculata* (Heel-Splitter) was not collected from the mainstream of the Illinois River in 1966, but one living specimen was taken in a bottomland lake adjoining the river.

[b] Not reported from the mainstream of the Illinois River.

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[1] The 1870-1900 and 1906-1912 periods were chosen arbitrarily and were not necessarily inclusive dates of the occurrence of a mussel species in the Illinois River. However, at some time during a period in which a species was listed as present, it was known to have occurred in the river.

tirpated from the mainstream of the Illinois.

In the 1966-1969 period only 24 kinds of mussels were taken alive, indicating

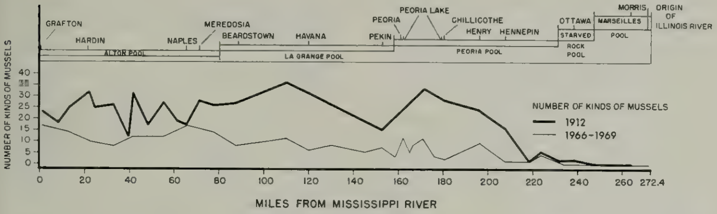

Fig. 9.—Kinds of living mussels taken in the Illinois River in 1912 and in the 1966-1969 period. Note that by 1912 pollution already had affected the mussel fauna of the upper part of the river and that by 1966 the mussel fauna of virtually the entire river had been affected. In the lower part of the river the mussel fauna changed less than it did in the remainder of the river between 1912 and 1966. In 1966 the commercial mussel fishery was confined to the lower 87 miles of the river, but in 1969 it was resumed in the vicinity of Peoria.

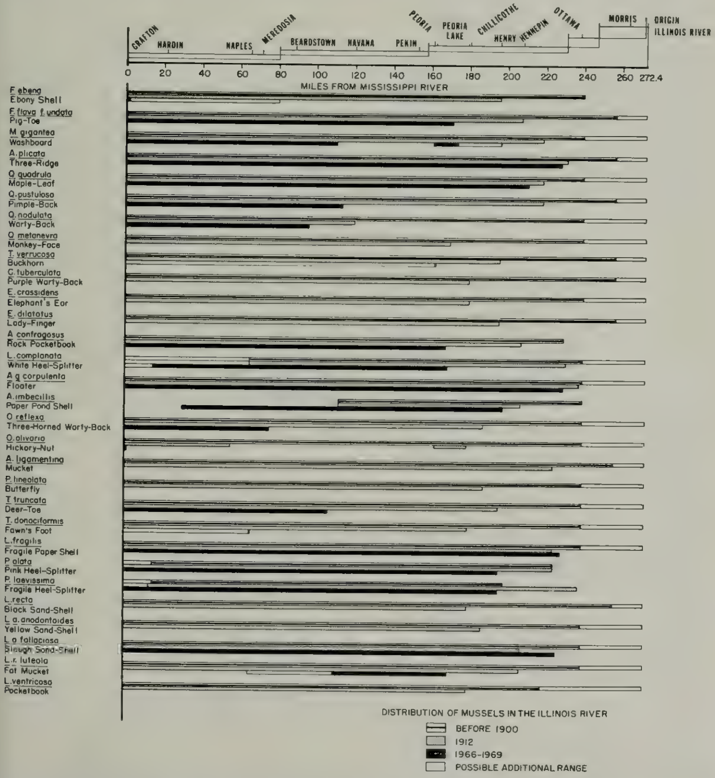

Fig. 10.—Changes in the distribution of the more common mussels of the Illinois River from before 1900 to the 1966-1969 period. Note that some of the formerly common kinds of mussels were not taken alive in the 1966-1969 period. The possible additional ranges of the mussels were based on the author's opinion and were not substantiated by records.

that during the past three-quarters of a century 25 kinds of mussels have been extirpated from the Illinois River and its adjoining bottomland lakes (Tables 5, 9, and A-3)[1]. Data presented in the preceding section indicated that most of these mussels were not eliminated from the river until after 1912 (Fig. 9). However, by 1912 the distribution of most of the mussels had been reduced, and since 1912 further reductions have occurred in the distribution and abundance of most of the surviving kinds of mussels in the river (Fig. 10). Five (*F. ebena, A. suborbiculata, O. olivaria, T. donaciformis,* and *C. parva*) of the 24 kinds of living mussels taken in the present study were represented by only single specimens.

In this section the author has attempted to recapitulate the effects that domestic, industrial, and agricultural pollution have had upon the mussel fauna of the various parts of the Illinois River since the 1870-1900 period. Untreated domestic and industrial wastes were being emptied into the river and its tributaries before 1900. In 1900 the pollution load of the river was increased greatly following the opening of the Chicago Sanitary and Ship Canal. No doubt, some species of mussels had been affected adversely by pollution in certain localities of the river even before 1900.

Upper River

The upper Illinois River as designated here extends from its source at the confluence of the Des Plaines and Kankakee rivers (river mile 272.9) downstream to the Starved Rock dam (river mile 231.0) near Utica (Fig. 1). This upper portion of the river encompasses the lower 1.4 miles of the Dresden pool, the Marseilles pool, and the Starved Rock pool.

In the 1870-1900 period there were at least 38 different kinds of mussels living in the upper river (Table A-21), whereas in 1966 none were collected there. In the early 1870's Calkins (1874: 11) found that:

> "At the Starved Rock and in its vicinity, the river, here shallow, is literally filled with clams lying half buried in the sandy bottom."

Since 1933 this section of the river has been impounded by the Starved Rock dam.

A drastic change began to occur in the river in 1900 following the opening of the Chicago Sanitary and Ship Canal. Lake Michigan water, laden with sewage and untreated industrial wastes from the Chicago area, flowed into the Des Plaines River and thence into the upper Illinois, a distance of about 57 river miles from Chicago. In 1909 Wilson & Clark (1912:34) noted that:

> "The Des Plaines River, which joins the Kankakee to form the Illinois River, is simply an immense sewer bringing down the Chicago drainage. Both rivers, but especially the Des Plaines, are full of the characteristic algae and other vegetation which grow in such waters, and the combination of a copious vegetation with the sewage has effectually killed off all the mussels in the vicinity. Not a single living specimen could be found in either river, but there were hundreds of dead shells along the banks, most of them old and well bleached but still capable of identification."

In 1912 in the vicinity of Morris (63 river miles from Lake Michigan) Forbes & Richardson (1913:517) found no mussels living in the heavily polluted mainstream; however, they did take seven species of dead mussels there. A little farther downstream they (1913: 518) observed that:

> "In midsummer, 1911, the water at the Marseilles dam had a grayish look and a disagreeable odor, but with perceptibly less material in suspension than at Morris."

Forbes & Richardson (1913:525) in 1912 reported that at about 7 miles below the Marseilles dam at Ottawa there was a lessening of contamination. They stated that:

> "Diligent use of the crow-foot

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[1] The author was aware of the possibility that one or more rare species may have been missed in the 1966-1969 study; however, for purposes of this paper he has treated any kind of mussel formerly occurring in the river but not taken alive during the 1966-1969 period as having been extirpated from the river.

> dredge in various situations brought to light no living mussels except on a bar in Fox River water just outside the mouth of that stream. Here two species were obtained alive—*Lampsilis ventricosa* and *L. laevissima*—and dead shells of eight other species. . . . The number of dead shells of both Unios and univalves, as compared with the living specimens found, was indicative of an environment still difficult for mollusks."

By 1912 pollution had virtually eliminated the mussel population of the river in the vicinity of Starved Rock (Forbes & Richardson 1913:527–528). From this part of the river in the early 1870's Calkins (1874) collected 35 kinds of mussels (recognized by the present author), whereas in 1912 Forbes & Richardson (1913:528) found living specimens there of only two species of mussels (*A. plicata* and *L. complanata*).

During the summer months dissolved oxygen in the upper river in the 1911-1928 period was extremely low, ranging from 0.1 to 0.9 ppm (Mills, Starrett, & Bellrose 1966:9). Probably the upper river's low dissolved oxygen content was an important factor reducing the mussel popuation during at least the first part of this century. As indicated in Table A-2 and Fig. 11, the dissolved oxygen in the upper river is now relatively high as compared to that of the 1911-1928 period, except possibly following a heavy rainstorm in the Chicago area. During such a storm the capacities of the combined interceptor sewers and of the treatment plants may be exceeded, and polluted waters are then discharged into the waterway.

Forbes & Richardson (1913:507) described the deplorable condition of the upper river at Morris in 1912:

> "The water here was grayish, sloppy, and everywhere clouded with tufts of *Sphaerotilus* and *Carchesium*. The odor was continuously foul, with a distinct privy smell in the hottest weather. Bubbles of gas were continually breaking at the surface from a soft bar of sludge . . . . On the warmest days putrescent masses of soft, grayish black, mucky matter, from the diameter of a walnut to that of a milkpan, were floating on the surface."

In 1966 the water at Morris and downstream from there had the appearance of that of a relatively clean stream. The water had only a slight chemical odor but not enough to deter the use of the river here by boaters, water skiers, and some bathers. However, the bacterial counts (Table A-1) indicated that the entire river in 1966 was unfit for swimming.

The vast improvements which have occurred in the dissolved oxygen content and the putrid condition of the upper river since the 1912-1928 period are, according to Mills, Starrett, & Bellrose (1966:9), a result of

> "the construction and operation of the tremendous sewage treatment plants by the Chicago Sanitary District through a program instituted in 1922, and the lock and dam system built in the 1930's which slowed up the movement of the water. The adoption of better water pollution laws by the state also had its effect."

The improvement in the treatment of domestic and industrial wastes in the past two decades by the cities along the Des Plaines, Kankakee, and upper Illinois rivers also has helped to reduce the biochemical oxygen demand in the upper Illinois. In spite of the amelioration in the dissolved oxygen content and the appearance of the water during the past 40 years, the upper river still provides a poor environment for fish and mussel life (Fig. 10 and 11; Tables 10 and A-3) (Mills, Starrett, & Bellrose 1966:11–13 & 14–17).

As mentioned earlier, no living mussel was taken in the upper river in the 1966 survey. This indicated that the upper river has remained unsuitabe even for reestablishing populations of mussel species possessing some tolerance to pollution. Such tolerant mussels are living only a short distance downstream in the Peoria pool (Table A-3). The dissolved oxygen determinations and crowfoot bar catches for the entire river (Fig. 11) indicated that in 1966 mussels were living in the lower La Grange pool in water containing less dissolved oxygen than was observed in the upper river.

The determinations of the maximum amounts of ammonia nitrogen (N) cited in this study were made in 1967 (Allan Poole, pers. comm., 11 March 1968).

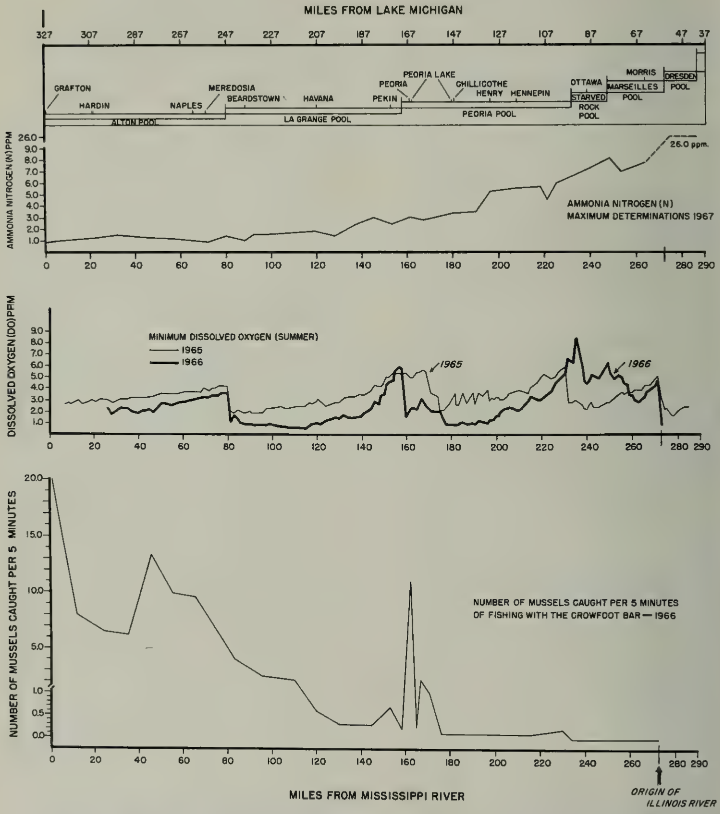

Fig. 11.—Maximum amounts of ammonia nitrogen (N) and dissolved oxygen in the Illinois River and numbers of mussels caught per 5 minutes of fishing with the crowfoot bar in the 1966 survey. The ammonia nitrogen (N) determinations were furnished by Mr. Allan Poole (pers. comm., 11 March 1968). The 1965 and 1966 dissolved oxygen determinations were made from water samples taken 3 feet below the surface of the river in the navigation channel by the author. Increases in the dissolved oxygen content of the river are apparent below the various navigation dams and in Peoria Lake. The 1966 crowfoot bar catches, expressed on a unit-of-effort basis, reflect the relative abundance of mussels in various parts of the river. (Mussels in Lower and Middle Peoria lakes were found to be more abundant than crowfoot bar collections indicated.) The steady upstream decline in the mussel population in the La Grange pool in 1966 apparently was associated with pollution from the Peoria-Pekin metropolitan area and in the upper part of the river with pollution from the Chicago-Joliet area. About 1 mile above Peoria (river mile 162.0) the mussel population increased markedly. Note the decline in the mussel population and the increase in ammonia nitrogen (N) upstream from Middle Peoria Lake.

Table 10.—Numbers of kinds of mussels occurring in the navigation pools of the Illinois River proper in the 1870-1900 period, in 1912, and in the 1966-1969 period.

Navigation Pool	*Kinds of Mussels*		
	1870–1900	1912	1966–1969
Alton	39	38	20
La Grange	41	38	17
Peoria	41	37	16
Upper River	38	4	0

The author has assumed that these 1967 maximum determinations were rather typical of the river for at least the preceding 5 years (Fig. 11). According to Barth *et al.* (1966:1211):

> "Contemporary American treatment plants are designed on the basis of solids and BOD removal with little regard to nitrogen transformation."

This point might well apply to phosphorus also. (No correlation appeared to exist between the abundance of mussels and amounts of total phosphates present in the river.) Industrial wastes and agricultural runoff also are involved here.

Possibly a high amount of ammonia nitrogen (N) has a deleterious effect on mussels similar to its supposed effect on fishes. According to Spicer (1952) ammoniacal nitrogen over 1 ppm in a river is not very attractive to fish, and if the value exceeds 5 ppm even few, if any, coarse fish will occur in the stream. Ellis (1937:393) found that waters containing 2.0–3.0 ppm of ammonia and supporting a good fish fauna had high dissolved oxygen contents (5.5–7.0 ppm). The maximum determinations of ammonia nitrogen (N) exceeded 6.0 ppm throughout the upper river, and in this section no living mussels were found in 1966. As indicated in Fig. 11 and Table A-3, in 1966 mussel life began to appear in the river below the Starved Rock dam where the maximum amount of ammonia nitrogen (N) did not exceed 6.0 ppm. This relationship between mussel life and ammonia nitrogen (N) in the river may be considered either suggestive or accidental. The chemistry of a polluted river, such as the Illinois, is, in the author's opinion, too complex to allow one to infer from field data that one chemical or condition was the sole limiting factor.

It is apparent from the data shown in Fig. 11 that various pollutants, such as heavy metals (Wurtz 1962:54), possibly including ammonia nitrogen (N), adversely affected mussel life in the Illinois. The distance and time required for at least partial dissipation of domestic and industrial pollutants below the Chicago-Joliet and Peoria-Pekin metropolitan areas were reflected by the absence, presence, and abundance of certain species of mussels (Fig. 11; Table A-3). Experimental deletion-type bioassay studies with various life stages of living mussels and/or other aquatic organisms in river waters and bottom muds from which various pollutants could be eliminated (the opposite of the usual additive type of bioassay) might be extremely helpful to sanitary and industrial engineers. Such analyses might isolate the key pollutants limiting mussels and other aquatic life in a stream, thereby greatly reducing costs in the construction and operation of advanced waste treatment plants.

Thompson (1928:301) reported that fish life was eliminated by pollution from the upper river between 1912 and 1917; however, by the early 1940's some species of fishes had become reestablished in the upper river (INHS files). In the late 1950's and the 1960's many of the important host fishes of mussels were scarce in the upper river as indicated by the author's electrofishing data presented in Table 11. The only common endemic fishes taken regularly in the upper river were emerald shiners, *Notropis atherinoides* Rafinesque, and black bullheads, *Ictalurus melas* (Rafinesque). The most abundant fishes in the upper river were carp; goldfish, *Carassius auratus* (Linnaeus); and carp-goldfish hybrids (Fig. 12). Evidently these exotic Asiatic fishes have been able to adapt to the adverse conditions of the upper river. Whether mussels can use these abundant exotic species in the river as host fishes was not known to the author. However, even

Table 11.—Average numbers of common host fishes of mussels caught per 30 minutes of electrofishing in the navigation pools of the Illinois River (1962–1966).

Kind of Fish	*Alton Pool*	*La Grange Pool*	*Peoria Pool*	*Starved Rock Pool*	*Marseilles Pool*
Channel catfish	3.73	1.42	0.09	0.52	0.00
Freshwater drum	1.16	1.01	0.20	0.04	0.03
Sunfishes (Centrarchidae)[a]	8.31	16.99	13.41	0.40	0.71

---

[a] Includes rock bass; warmouth, *Lepomis gulosus* (Cuvier); green sunfish; pumpkinseed; orangespotted sunfish; bluegill; sunfish hybrids; smallmouth bass; largemouth bass; white crappie; and black crappie.

though the known host fishes usually were scarce, in the upper river, the author believed that sufficient numbers of fishes carrying glochidia during the past decade could have moved into the upper river either from tributaries or from downstream to have restocked the river with at least a few species of mussels had the environment otherwise been suitable for mussels. Evidence that tributaries may be mussel sources appeared in 1966 when four species of live mussels were collected in the Aux Sable River near its mouth where the stream empties into the Marseilles pool.

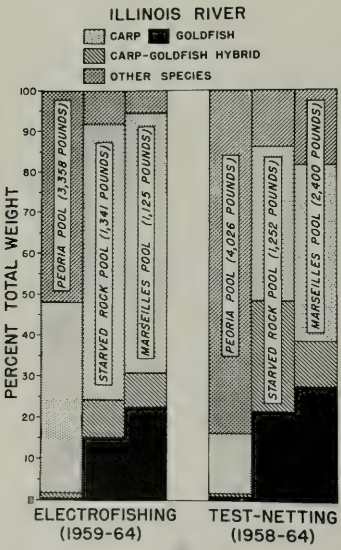

Fig. 12.—Fishes taken with the electric shocker and with 1-inch wing nets in the Peoria, Starved Rock, and Marseilles navigation pools of the Illinois River. Note that the catches in the upper river (Marseilles and Starved Rock pools) were dominated by carp, goldfish, and carp-goldfish hybrids, whereas in the adjacent downstream Peoria pool endemic species formed an important part of the catches.

Siltation in the upper river was minor as compared with that in the Alton pool where mussels were abundant enough to support a commercial fishery in 1966 (Fig. 11). The navigation dams possibly have reduced the flow of the current enough to make the environment in the river unsuitable for the reestablishment of several current-inhabiting species of mussels present before 1900. However, the reduction in current would not have been sufficient to have prevented the reestablishment of a number of other species still found in the remainder of the channelized river.

It appeared from this study, that in spite of the tremendous efforts made since the 1920's by Chicago and other cities and by industries along the Illinois River waterway to initiate and later to improve the treatment of wastes, the upper river evidently remained unsatisfactory for mussel life.

Peoria Pool

The Illinois River flows from the upper river through and over the Starved Rock lock and dam into the Peoria pool and continues 51.8 miles downstream to below Chillicothe where it widens abruptly into two shallow fluviatile lakes (Type 49) known as Upper (or Upper and Middle) and Lower Peoria lakes (about 1.5 miles average width). The river here is two lakes for 16.4 miles of the navigation channel except at the Peoria Narrows (Fig. 13) where an alluvial fan separates the lakes. At Peoria the river constricts to a normal width of about 0.17 mile and continues 5.2 miles downstream to the Peoria dam.

Since 1870 at least 41 kinds of mussels (Table A-21) have been known to occur in the Peoria pool (73.4 miles long). In the 1966-1969 period 16 kinds of mussels were found living in the Peoria pool. However, in the upper 56.1 miles and lower 1.9 miles of this pool living mussels were relatively scarce as compared with the numbers found in the remainder of the pool (Table A-3 and Fig. 11). The extirpation of 25 kinds of mussels together with reductions in the distribution and abundance of the surviving kinds probably occurred here mainly after 1912 rather than before, as was the case in the upper river.

Starved Rock Dam to Chillicothe.—Between 1871 and 1900 some pollutants from Chicago were coming into the Illinois River at La Salle (Fig. 1) through the Illinois and Michigan Canal (Kofoid 1903:201–202; Walker 1956:6). Concerning pollution in the Starved-Rock-dam-to-Chillicothe section of the Peoria pool in 1911 and 1912, Forbes & Richardson (1913:543–544) reported that:

> "It was at Spring Valley, fifty-seven miles below the mouth of the Des Plaines, that, in summer time, the last visible symptoms of water pollution were to be seen. The water here had not yet recovered its normal slightly greenish tint, but was still grayish with suspended specks of septic and pollutional plankton; and it still smelled slightly of sewage, in part no doubt because of local contamination from Peru and La Salle, a few miles above. . . . A considerable variety of aquatic insect larvae, of living mussels, and of gastropod mollusks, and a much smaller proportion of dead shells, testified further to an improved environment. . . .
>
> At Hennepin it may be fairly said that virtualy normal conditions were found, except for the state of the bottom in winter time; although it must be confessed that our chemical data, especially those for the mid-

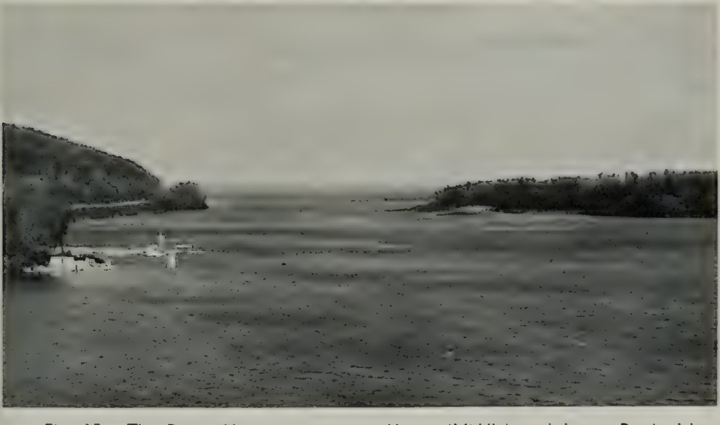

Fig. 13.—The Peoria Narrows, separating Upper (Middle) and Lower Peoria lakes. Upstream beyond the Narrows is Upper (Middle) Peoria Lake. Photo by the author.

> summer low-water of 1911, were hardly consistent with this statement. . . .
>
> *Henry to Chillicothe.* — In this, the last section of the upper Illinois systematically studied by us in 1911 and 1912, the process of renovation is simply carried a little farther on than in the Henry-to-Hennepin section just above. It is only in the winter time that the effects of pollution are manifest here to the senses . . . ."

By 1915 the river from Chillicothe upstream had unwholesome conditions in the bottom muds (Richardson 1921*b*: 33). In 1912 Richardson (1928:456) determined the dissolved oxygen to be about 3 ppm at Chillicothe, whereas in the early 1920's zero was the usual lower limit of oxygen at this site. According to Forbes & Richardson (1919:145):

> "More recent evidence of a still continued gradual creeping downstream of pollutional conditions is found by comparison of collections made in 1911 with those obtained in August, 1918. In the former year a foul-water fungus (*Sphaerotilus natans*) disappeared from both channel and shore at or near Starved Rock, while August 28 to 30, 1918, it was found in the river at Henry, 35 miles below Starved Rock, and also at Lacon, 6 miles still farther down."

During the 1914-1925 period evidently pollution was so severe in the Starved-Rock-to-Chillicothe section that all of the mussel life was eliminated. Richardson's Table XXI (1928:457) indicated that in the 1924-1925 period he took no live mussel above Upper Peoria Lake (Table 12).

The increase in pollution after 1912 in this section of the river as well as farther downstream was related to several factors which developed in the Chicago area. In the 1914-1920 period, according to Richardson (1928:398):

> "the Chicago population is estimated to have increased around 10 per cent, to about 2,701,000; and the stock yards wastes, in population equivalent equal to 1,040,000, were about 19 per cent greater than in 1914, after having fallen off 353,000 since the peak of the war-time activity of 1918. Between 1914 and 1920, all of the wastes from the sources above described were received by the Sanitary Canal and Illinois River wholly untreated and subject after delivery only to the effects and processes of dilution and biological purification, varying with river levels, temperature, and other physical conditions, as chance might offer."

Other untreated wastes from the Chicago area in this period were estimated by Richardson (Ibid.) to have had an additional population equivalent of about 500,000.

In the 1920's the additional sewage from the expanding human population of the Chicago area began to be affected by the treatment of sewage and the reduction of certain industrial wastes entering the canal (Richardson 1928:399). By 1960 the wastes before treatment in the Chicago metropolitan area had a population equivalent of 9.50 million, but after treatment they amounted to a population equivalent of only 1.15 mil-

Table 12.—Numbers of kinds of mussels living in various parts of the Peoria navigation pool of the Illinois River in 1912, the 1924-1925 period, and the 1966-1969 period.

Location	*Kinds of Living Mussels*		
	1912[a]	1924–1925[b]	1966–1969[c]
La Salle-Peru	5	0	4
Spring Valley	1	0	1
Hennepin	17	0	1
Henry	24	0	9
Chillicothe	28	0	2
Peoria Lake	35	16	12

[a] Forbes & Richardson (1913:529–536); Danglade (1914:37).
[b] Richardson (1928:455 & 457, Tables XX and XXI). From the latter table the author inferred that no mussel life existed in the river in 1924–1925 above Upper Peoria Lake.
[c] Present study.

lion (United States Public Heath Service 1963: III-3). This fact indicated a reduction of about 77 percent since 1918 in the wastes entering the Illinois River waterway from the Chicago area. This is a remarkable engineering achievement, for the population equivalent of wastes before treatment in 1960 was about double the population equivalent of 1918.

In the 1966 survey 32 living mussels were taken in the Starved-Rock-to-Chillicothe section of the Peoria pool (Table A-3). Ten different kinds of mussels were represented in these collections of which 50.0 percent were three-ridges (*A. plicata*) and floaters (*A. g. corpulenta*). The presence of living mussels in 1966 in this section of the river indicated an improvement in conditions for mussels since the 1918-1925 period. The dissolved oxygen content of the river in the lower part of this section of the Peoria pool tended to be quite low in midsummer (Fig. 11); however, the author has never recorded zero readings as did Richardson (1928:456) at Chillicothe in the early 1920's. The maximum determinations of ammonia nitrogen (N) (range 3.4–6.0 ppm) in this section of the river did not exceed 6.0 ppm in 1967 as they did in the upper river where no living mussel was taken in 1966 (Fig. 11). The range of maximum total phosphates (PO_4) in this section of the river in 1967 was 2.5–5.5 ppm.

La Salle-Peru.—In 1912 Forbes & Richardson (1913:529) collected mussels between Utica and Peru with a crowfoot bar and wrote that:

> "The large proportion of dead specimens, as compared with the ratios obtained farther down the stream, indicate unfavorable conditions for mussels in the stretch of river between Utica and Peru."

A comparison of the numbers and kinds of mussels taken in 1912 and 1966 was made in Table 13. Two of the four kinds of mussels taken in 1966 in this area were also collected there by Forbes & Richardson. With the exception of the mucket (*A. ligamentina*), the other species taken alive there in 1912 were found a short distance downstream in 1966. The mucket was not collected alive anywhere in the Illinois River in the present

Table 13.—Numbers and kinds of mussels taken alive and dead in the LaSalle-Peru area of the Illinois River in 1912 and 1966.

Kind of Mussel	*Mussels Taken*		
	1912[a]		1966[b]
	Alive	Dead	Alive
F. ebena (Ebony Shell)	0	1	0
A. plicata (Three-Ridge)	5	3	1
Q. pustulosa (Pimple-Back)	0	1	0
Quadrula sp.	0	3	0
L. complanata (White Heel-Splitter)	1	2	0
A. g. corpulenta (Floater)	0	0	1
S. undulatus (Squaw Foot)	0	1	0
O. reflexa (Three-Horned Warty-Back)	0	1	0
A. ligamentina (Mucket)	4	3	0
L. fragilis (Fragile Paper Shell)	1	1	2
P. alata (Pink Heel-Splitter)	1	4	0
L. a. f. *fallaciosa* (Slough Sand-Shell)	0	0	2
L. ventricosa (Pocketbook)	0	4	0
Totals	*12*	*24*	*6*

[a] Forbes & Richardson (1913:530).
[b] Present survey (river miles 220.7–229.3).

study, and the author was surprised to learn that this species was able to survive the poor conditions existing for mussels in this part of the river in 1912.

A floater (*A. g. corpulenta*) was collected just below Utica at river mile 229.3, the farthest upstream point where a live mussel was taken in 1966. In the La Salle-Peru area the maximum ammonia nitrogen (N) determination in 1967 was 6.0 ppm (Fig. 11), and as was shown in Table 13, a few specimens of four kinds of mussels were able to withstand this high concentration of ammonia nitrogen for at least a short time. The author has found that the midsummer dissolved oxygen content of the river in this area usually has been over 4.5 ppm (Fig. 11). The relatively high oxygen content of the river here is caused by the water mixing with the air as it falls over the Starved Rock dam just upstream from the La Salle-Peru area. As has been discussed for the upper river, the author does not consider dissolved oxygen a limiting factor for mussels in the La Salle-Peru section of the river.

Hennepin.—In the Hennepin area in 1912 Forbes & Richardson (1913:533) collected 187 living mussels of 17 different kinds (Fig. 9). These collections included in part 60 slough sand-shells (*L. a.* f. *fallaciosa*), 45 three-ridges (*A. plicata*), 23 white heel-splitters (*L. complanata*), 14 floaters (*A. g. corpulenta*), and 11 washboards (*M. gigantea*). In 1966 only one live three-ridge (*A. plicata*) was taken in this part of the river.

Henry.—Forbes & Richardson (1913: 533 & 536) and Danglade (1914:37) reported taking 24 different kinds of live mussels in the Henry area in 1912, but in 1966 only 9 kinds were collected alive there (Table A-22). Danglade (1914:14) took 128 living mussels there in 1 hour of fishing with a crowfoot bar, whereas in 3 hours of similar fishing in 1966 only 4 live mussels were caught (Table 14). The comparison in Table 14 of crowfoot bar catches made in 1912 and 1966 clearly reflected the impact of pollution on the mussel population in this part of the river during the intervening 54 years.

Chillicothe.—From the river near Chillicothe in 1912, Forbes & Richardson (1913:533 & 536) and Danglade (1914:

Table 14.—Numbers and kinds of live mussels taken with the crowfoot bar in the Illinois River in the vicinity of Henry in 1912 and 1966.

Kind of Mussel	*Mussels Taken in 1 Hour of Fishing in 1912*[a]	*Mussels Taken in 3 Hours of Fishing in 1966*[b]
F. f. f. *undata* (Pig-Toe)	5	0
M. gigantea (Washboard)	4	0[c]
A. plicata (Three-Ridge)	70	0[c]
Q. quadrula (Maple-Leaf)	2	0
Q. pustulosa (Pimple-Back)	5	0
T. verrucosa (Buckhorn)	1	0
E. dilatatus (Lady-Finger)	1	0
A. confragosus (Rock Pocketbook)	2	0
L. complanata (White Heel-Splitter)	2	0
A. g. corpulenta (Floater)	2	2
S. undulatus (Squaw Foot)	1	0
A. ligamentina (Mucket)	25	0
T. truncata (Deer-Toe)	1	0
L. fragilis (Fragile Paper Shell)	4	1
P. alata (Pink Heel-Splitter)	2	0[c]
L. a. f. *fallaciosa* (Slough Sand-Shell)	1	1
Total	*128*	*4*

[a] Danglade (1914:14). The collection may have been made in 1911; however, in this paper the author has used only the 1912 date.

[b] Present survey. Collections from river miles 190.0–199.3.

[c] This mussel was taken here in 1966 either by dredging or wading. Also collected here in 1966 either by dredging or wading were *A. g. grandis* (Floater), *A. imbecillis* (Paper Pond Shell), and *P. laevissima* (Fragile Heel-Splitter).

37) reported collecting 28 different kinds of mussels (Table A-22). Danglade (1914:15) caught 223 mussels with a two-bar haul over the lower end of a productive mussel bed located just above Chillicothe. Part of his catch included 83 three-ridges (*A. plicata*), 25 fat muckets (*L. r. luteola*), 24 washboards (*M. gigantea*), 22 lady-fingers (*E. dilatatus*), 17 pimple-backs (*Q. pustulosa*), 17 pig-toes (*F. f.* f. *undata*), and 12 muckets (*A. ligamentina*). Danglade (Ibid.) mentioned that in earlier years 10–12 ebony shells (*F. ebena*) had been caught per haul from this bed by commercial clammers, whereas in 1912 only an occasional ebony shell was taken. Probably by 1918 this mussel bed had been wiped out by pollution, and apparently conditions have never been favorable enough since for the bed to become reestablished. In this area in 1966 the only living mussels taken were five three-ridges (*A. plicata*) and one slough sand-shell (*L. a.* f. *fallaciosa*).

Peoria Lake.—The mussel life in the broad expanse of Peoria Lake between Chillicothe and Peoria was described in 1911 and 1912 by Danglade (1914:14):

> "The slow current, the large volume of water, the good average depth and soft mud bottom are suitable for mussel growth, and there are consequently many fine mussel beds and an enormous quantity of shells, making this at present probably one of the best mussel-producing districts in the United States."

During that period at least 35 different kinds of mussels lived in Peoria Lake (Table A-23).

Between the 1913-1915 period and 1920 pollution had virtually eliminated the former normal bottom animals of the river between Chillicothe and Beardstown, including those of Peoria Lake (Richardson 1925*a*:327). This encroachment of pollution from upstream and its effects on the mussel life of Peoria Lake were described by Richardson (1928:454):

> "The mussels died out rapidly in all three sections of the lake during and after 1917 until commercial clamming entirely ceased because of failure to obtain shells. In the summer of 1920 a single clammer operated a bar for a few days in the channel of the Lower Lake opposite the center of Peoria, but took nothing but dead shells except for an occasional live specimen of *Amblema rariplicata* or still less frequently *Quadrula pustulosa.* In 1920-1922 the Natural History Survey took single examples of three species (*Amblema rariplicata, Anodonta imbecillis,* and *Quadrula pustulosa*). . . . Commercial clamming on a scale much reduced from that of the pre-1920 period began again in 1924 and has been continued sporadically by a few clammers since. The only commercial species obtained since then in salable quantity, however, has been the common three-ridge, *Amblema rariplicata.*"

Dr. Morrison (pers. comm., 12 August 1969 and 6 March 1970) wrote that there was very little mussel life in Peoria Lake in 1931 and that he took only three living mussels there.

In this study 12 different kinds of mussels were taken alive in Peoria Lake, indicating that at least 23 kinds had been extirpated from this part of the river since 1912 and 4 since the 1924-1925 period (Tables A-3, A-23, and 15).

Richardson (1928:455) considered Upper Peoria Lake as two separate lakes —Middle Peoria Lake (river miles 167.2–174.9) between the Peoria Narrows and Spring Bay, and Upper Peoria Lake (river miles 174.9–179.7) from Spring Bay to below Chillicothe. The author has followed Richardson's division of Upper Peoria Lake into two lakes in order to compare his 1924-1925 mussel collections with those made in the present study (Table 15). Even though his division of Upper Peoria Lake into two lakes was artificial, this separation was useful in treating the 1966 data of this lake.

Apparently Upper Peoria Lake as designated here with its broad expanse of water and virtual absence of current tended to serve as a partial recovery zone for the river. The dissolved oxygen curves shown in Fig. 11 clearly indicated a sharp increase in the dissolved oxygen

Table 15.—Kinds of mussels present in Peoria Lake in the 1924-1925 and 1966-1969 periods.[a]

Kind of Mussel	*Mussels in Peoria Lake*			
	Upper		Middle and Lower	
	1924–1925	1966–1969	1924–1925	1966–1969
F. f. f. *undata* (Pig-Toe)	P[b]	A	P	P
M. gigantea (Washboard)	A	A	A	P
A. plicata (Three-Ridge)	P	A	P	P
Q. quadrula (Maple-Leaf)	P	A	P	P
Q. pustulosa (Pimple-Back)	A	A	P	A[c]
E. dilatatus (Lady-Finger)	A	A	P	A
A. confragosus (Rock Pocketbook)	A	A	A	P
L. complanata (White Heel-Splitter)	P	A	A	P
A. g. grandis (Floater)	A	A	A	P
A. g. corpulenta (Floater)	P	P	P	P
A. imbecillis (Paper Pond Shell)	P	A	P	A
A. suborbiculata (Heel-Splitter)	A	A	P	A
O. reflexa (Three-Horned Warty-Back)	A	A	P	A
L. fragilis (Fragile Paper Shell)	A	A	P	P
P. alata (Pink Heel-Splitter)	A	A	P	A
P. laevissima (Fragile Heel-Splitter)	A	P	P	P
C. parva (Liliput Shell)	A	A	P	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P	P	P
L. r. luteola (Fat Mucket)	P	A	P	P
Total	*8*	*3*	*15*	*12*

[a] Richardson (1928:455), 1966 survey, and 1969 commercial data.
[b] P denotes present and A designates absent.
[c] Taken by commercial fisherman in 1969 from the Illinois River just below Peoria Lake.

content of the river at the upper end of Middle Peoria Lake (river mile 174.9). Likewise, in coming downstream in the 1966 survey the first relatively large-sized population of mussels was encountered in Middle Peoria Lake (Fig. 11 and Table A-3). In Upper Peoria Lake in 1966 only 6 live mussels of 3 species were collected, whereas in Middle Peoria Lake 533 live mussels of 11 different kinds were taken.

In the 1924-1925 period Richardson (1928:455) collected eight kinds of mussels from Upper Peoria Lake, all taken at its lower end. Richardson (Ibid.) was of the opinion that the 11 species of mussels he took in the 1924-1925 period in Middle Peoria Lake (Table 15) probably had remained "through the worst of the wave of pollution that destroyed the more sensitive *Mollusca* about ten years ago." In the 1924-1925 period Richardson (1928:455) collected the liliput shell (*C. parva*) in Middle Peoria Lake and the three-horned warty-back (*O. reflexa*) in both Middle and Lower Peoria lakes. In 1966 both of these species were confined to the lower part of the river. Evidently the adults of these species were able to withstand the severe pollution in Peoria Lake during the period of World War I but were unable to maintain populations in subsequent years.

In 1966, beds comprised largely of three-ridges (*A. plicata*) were found in Middle and Lower Peoria lakes, and these beds were extensive enough to interest commercial mussel fishermen. No commercial fishing had been conducted in the Peoria pool for a number of years prior to 1969. In that year commercial mussel fishermen removed about 100,000 pounds of mussels (10 percent dead shells) from Lower and Middle Peoria lakes; however, 85,941 pounds (10 percent dead shells) of these mussels were dredged from one bed at river mile 164.1 (LB) in Lower Peoria Lake (Webb Moss, pers. comm., 30 October 1969). They also found mussels occurring abundantly in Middle Peoria Lake but did little fishing there in 1969. The 1966 survey data and the above commercial statistics indicated that mussels were much more abundant in Middle and Lower Peoria lakes in the 1966-1969 period than they were in the 1918-1931 period. The author is of the opinion that through the years natural selection has played an important role in reestablishing the mussel beds in Peoria Lake. Improved treatment of municipal and industrial wastes in the Chicago area and elsewhere along the upper Illinois River waterway have also undoubtedly helped to improve Peoria Lake as a mussel habitat. However, conditions had not improved enough in Peoria Lake to permit the reestablishment of 23 kinds of mussels known to have lived in this part of the river in 1912.

Foot of Peoria Lake to Peoria Dam.—The Illinois River abruptly narrows at Peoria and flows downstream 5.2 miles to the Peoria lock and dam. A power plant (fossil fuel) is located on the left bank of the upper end of this section of the river, and it has not been determined what effect the heated discharge from this plant has on mussel life in this section of the river. However, on the left bank of the upper part of this section of the river (river miles 161.1–162.3) occurred the largest standing crop of living mussels found in the entire river in the 1966 survey (at river mile 161.6 total phosphates were 5.7 ppm, and ammonia nitrogen was 3.0 ppm). The estimated standing crop here in 1966 was 6,040 pounds (live weight) of mussels per acre. The three-ridge (*A. plicata*) comprised 85.3 percent of the mussels taken here in the 1966 survey. In 1969 commercial mussel fishermen removed from these unfished waters 108,500 pounds (live weight) of mussels (Webb Moss, pers. comm., 30 October 1969). In the 1966-1969 period 11 kinds of mussels were collected from the upper part of this section of the river, including the pimpleback (*Q. pustulosa*) and the buckhorn (*T. verrucosa*). Conditions evidently were better here for mussels than they were in Middle and Lower Peoria lakes; however, the differences were not as great as was indicated by the 1966 crowfoot bar catch data shown in Fig. 11. Catches in Peoria Lake would have been much higher had there been more current there (the current is not perceptible in Peoria Lake at normal pool stage), since the crowfoot bar is less efficient in slack water than in moving water. No sampling was done in this section between river miles 160.0 and 161.1.

The lower part of this section of the river (river miles 158.1–160.0) was below the outlets of the treated sewage and industrial effluents from East Peoria and Peoria. The demarkation between the upper and lower parts of this section of the river was reflected by a sharp decline in the mussel population (Fig. 11). In the upper part of this section of the river (river miles 161.1–162.3) the crowfoot bar catch was 11.0 mussels per 5 minutes of fishing, whereas in the lower part the catch was only 0.2 mussel per 5 minutes of fishing (Fig. 11; Table A-3). In 1966 wastes from East Peoria received only primary treatment. The city of Peoria has had a modern sewage treatment plant (river mile 160.2) for a number of years, and in the late 1960's it began tertiary treatment. In 1966, according to Mr. Edwin Fall of the Greater Peoria Sanitary District (pers. comm., 24 February 1969), the untreated wastes coming into the Peoria treatment plant had a population equivalent of 381,000, but the treated wastes going into the river had a population equivalent of 57,000.

La Grange Pool

The additional pollution load discharged into the river from the Peoria-Pekin area had a noticeable effect upon the mussel life in the upper part of the La Grange pool in 1966 (Fig. 11). In 1960 the estimated BOD load discharged into the river from industrial sources in the Peoria-Pekin area had a population equivalent of 386,000 (United States Public Health Service 1963: III-5). Mr. Edwin Fall (pers. comm., 24 February 1969) informed the author that the estimated population equivalent of treated and untreated domestic and industrial wastes entering the river in 1960 from Peoria was about 100,000, but as indicated above, this has been reduced considerably since 1960. The remaining 150 miles of the river from Pekin to Grafton received only agricultural runoff and effluents from small communities and a few small industries.

Kofoid (1903:198–203) reported that in 1897 sewage from Chicago entering the Illinois River through the Illinois and Michigan Canal at La Salle and from the Peoria-Pekin area was one of the most important factors causing an abundance of plankton in the Havana area. Apparently pollution did not become detrimental to aquatic life in the La Grange pool until after 1915 (Richardson 1921*b*:49). Richardson (1925*b*: 411) limited his collecting to small bottom fauna organisms in the La Grange and Alton pools, and as a result, the effects of pollution in the 1915-1920 period on mussel life in these pools were not recorded. Between the 1913-1915 period and the summer of 1920 the dissolved oxygen at Havana dropped from 4 ppm to 1 ppm (Richardson 1925*a*: 327–328). During this period pollution eliminated about 70 kinds of benthic organisms other than mussels from the river near Havana and 24 or more kinds between Havana and Beardstown (Richardson 1925*b*:410–413) (Fig. 14). In 1917 Richardson (1925*a*:329) observed a heavy mortality of snails in various parts of the river between Spring Valley and Havana.

Between 1870 and 1912 at least 43 different kinds of mussels were known to have occurred in the mainstream of the La Grange pool (Table A-21), whereas only 18 kinds were collected alive from the mainstream of this pool in 1966 (Table A-3). No doubt this drastic reduction in the mussel fauna of this pool occurred largely in the 1915-1920 period simultaneously with the destruction of other benthic organisms by domestic and industrial pollution from Chicago and the Peoria-Pekin area as described by Richardson (1921*a*, 1921*b*, 1925*a*, 1925*b*, and 1928). Silt pollution probably also has affected certain species of mussels in the La Grange pool, such as the yellow sand-shell (*L. a.* f. *anodontoides*).

Peoria Dam to Havana.—In 1912 Danglade (1914:17) found five mussel beds between Peoria and Pekin and sev-

Fig. 14.—The Illinois River at Beardstown, showing a towboat moving upstream. This section of the river is in the La Grange navigation pool. Photo by the author.

eral beds between Pekin and Havana. No mussel bed was detected in this section of the La Grange pool in 1966. Danglade (1914:18) determined the species composition of mussels in the Liverpool area of the river (between Pekin and Havana) in 1912 to be 36 percent three-ridges (*A. plicata*), 30 percent pimple-backs (*Q. pustulosa*), 5 percent washboards (*M. gigantea*), 4 percent muckets (*A. ligamentina*), 8 percent other commercial shells, and 17 percent noncommercial shells. In that area in 1966 only 36 living mussels of the following kinds were collected: 22.2 percent maple-leafs (*Q. quadrula*), 13.9 percent three-ridges (*A. plicata*), and 63.9 percent noncommercial species (Table A-3).

In the mainstream of the river between the Peoria dam and Havana 32 kinds of mussels were taken in 1912 by Danglade (1914:37), whereas only 11 kinds were collected from this section in 1966 (Table A-24). The 1966 collections from the mainstream of this section did not include five kinds of mussels taken alive that year in Quiver Lake (Table A-24). As has been mentioned earlier, Quiver Lake, located just above Havana, is merely a slough connected with the river. The lower part of the lake is a large expanse of the river. Natural springs on the bluff side (LB) of this lake evidently provided a more suitable habitat for mussels than did the mainstream; however, the species taken in Quiver Lake were collected in the river farther downstream.

Below Havana to La Grange Dam.—The size of the mussel population in 1966, as reflected by the crowfoot bar catches shown in Fig. 11, increased steadily as we proceeded downstream from below Havana (river mile 120.0). In 1966 a few washboards (*M. gigantea*), pimple-backs (*Q. pustulosa*), warty-backs (*Q. nodulata*), and deer-toes (*T. truncata*) appeared in the collections made in this section of the river (Fig. 10).

As the data in Fig. 11 indicate, the increase in the abundance of mussels in the lower part of the La Grange pool was accompanied by slight decreases in the maximum amounts of ammonia nitrogen (N). However, in this section of the pool the dissolved oxygen in midsummer sometimes becomes quite low (Table A-2 and Fig. 11). Low dissolved oxygen content and heavy siltation may have been important factors contributing to the loss of certain species of mussels since 1912 in this section of the river. The 1966 collections indicated that the mussel population there included 67.0 percent three-ridges (*A. plicata*) and 13.2 percent maple-leafs (*Q. quadrula*). These two abundant species the author considered somewhat tolerant of pollution and siltation.

In 1912 Danglade (1914:19–20) found pimple-backs (*Q. pustulosa*), washboards (*M. gigantea*), lady-fingers (*E. dilatatus*), and three-ridges (*A. plicata*) the most abundant species in this section. These species, excepting the lady-finger, were among the most abundant species found on downstream in the Alton pool in 1966 (Fig. 10; Tables 6, 7, and A-3). Another apparent effect of pollution and siltation in the lower La Grange pool since 1912 has been the extirpation of 23 different kinds of mussels (Table A-25).

Alton Pool

During the past three-quarters of a century 21 different kinds of mussels have been extirpated from this lower 80.2 miles of the river (Tables A-3 and A-21; Fig. 15). Concerning conditions in the Alton pool in 1912, Danglade (1914:7) commented:

> "Whether or not the great amount of sewage that is annually poured into the river is detrimental to the aquatic life in the lower stretches, the fact remains that from Chillicothe to near the mouth, with few exceptions, the Illinois is indeed a wonderfully productive stream in fishes and mussels, and far exceeds in these resources many rivers not having similar physical conditions."

In 1912 Danglade (1914:21–25) noted that some of the mussel beds in the upper part of the Alton pool were "playing out," but in the middle and lower parts of this pool the beds were very productive. Many of these beds were still pro-

Fig. 15.—The Alton navigation pool of the Illinois River at Hardin. Photo by the author.

ductive enough in 1966 to support a commercial mussel fishery. At least 38 different kinds of mussels were taken from this pool in 1912 by Danglade (1914:37), whereas only 20 kinds were collected there in the 1966 survey (Table A-3).

However, fewer species have been eliminated from the Alton pool than have been extirpated elsewhere in the river during the past 54 years (Fig. 10). Also, in 1966 mussels were much more abundant there than they were in the other pools except for one small area just below Peoria Lake and in Lower Peoria Lake (Fig. 11). Only in the Alton pool were conditions suitable in 1966 for the support of relatively large-sized populations of pimple-backs (*Q. pustulosa*) and washboards (*M. gigantea*) and moderate-sized populations of warty-backs (*Q. nodulata*) and three-horned warty-backs (*O. reflexa*). The species composition and abundance of mussels in the Alton pool in 1966 clearly indicated that by the time the water reached this pool some semblance of recovery in water quality had occurred although not enough to support the variety and numbers of mussels known to have existed there in 1912.

Richardson (1921*a*:405) noted that in the Alton pool:

> "Inside the 7-foot line in 1915 a soft light-colored silt 2 inches to more than 12 inches deep was found at most of our collecting stations."

Siltation probably has limited the distribution and abundance of such species as the yellow sand-shell (*L. a.* f. *anodontoides*) during the past 75 or more years in this pool. However, the prime limiting factor in the Alton pool probably has been the effects of domestic and industrial pollution from upstream sources.

A comparison of the collections of mussels made in the vicinity of Meredosia (river mile 71.2) between 1912 and 1966 indicated that the mussel fauna of the Alton pool was affected adversely by pollution between 1912 and 1930 but that conditions for mussels probably have worsened since 1930 (Table 16). Only single live specimens of the ebony shell (*F. ebena*), the fawn's foot (*T. donaciformis*), and the liliput shell (*C. parva*) were taken in the 1966 survey, and all of these were taken downstream from Meredosia. The paper pond shell (*A. imbecillis*) was not collected at Meredosia in 1966 but was taken just below there at Naples. In 1930 and 1955 the buckhorn (*T. verrucosa*) was present at Meredosia, but in the 1966-1969 period it was only taken farther upstream in the Peoria pool; however, the author believed that this species may still occur rarely in the Alton pool. The yellow sand-shell (*L. a.* f. *anodontoides*) was the only mussel taken in 1930 at Meredosia that was not collected alive from some location in the river during the 1966-1969 period (Fig. 10). This species

Table 16.—Kinds of mussels taken alive from the Illinois River in the vicinity of Meredosia in 1912, 1930, 1955, and 1966.

Kind of Mussel	*Mussels Taken*			
	1912[a]	1930[b]	1955[c]	1966[d]
F. ebena (Ebony Shell)	P[e]	P	A	A
F. f. f. *undata* (Pig-Toe)	P	A	A	P
M. gigantea (Washboard)	P	P	P	P
A. plicata (Three-Ridge)	P	P	P	P
Q. quadrula (Maple-Leaf)	P	P	P	P
Q. pustulosa (Pimple-Back)	P	P	P	P
Q. nodulata (Warty-Back)	P	P	P	P
Q. metanevra (Monkey-Face)	P	A	A	A
T. verrucosa (Buckhorn)	P	P	P	A
C. tuberculata (Purple Warty-Back)	P	A	A	A
P. cyphyus (Bullhead)	P	A	A	A
P. coccineum f. *solida*	P	A	A	A
E. crassidens (Elephant's Ear)	P	A	A	A
E. dilatatus (Lady-Finger)	P	A	A	A
A. confragosus (Rock Pocketbook)	P	P	P	P
L. complanata (White Heel-Splitter)	P	A	A	A
A. grandis complex (Floater)	P	P	P	P
A. imbecillis (Paper Pond Shell)	A	P	A	A
O. reflexa (Three-Horned Warty-Back)	P	P	P	P
A. ligamentina (Mucket)	P	A	A	A
P. lineolata (Butterfly)	P	A	A	A
T. truncata (Deer-Toe)	P	P	P	P
T. donaciformis (Fawn's Foot)	P	P	P	A
L. fragilis (Fragile Paper Shell)	P	P	P	P
P. alata (Pink Heel-Splitter)	P	A	P	P
P. laevissima (Fragile Heel-Splitter)	P	P	P	P
C. parva (Liliput Shell)	A	P	A	A
L. recta (Black Sand-Shell)	P	A	A	A
L. a. f. *anodontoides* (Yellow Sand-Shell)	P	P	A	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P	P	P
L. r. luteola (Fat Mucket)	P	P	P	A
L. ventricosa (Pocketbook)	P	A	A	A
L. o. f. *higginsii* (Higgin's Eye)	P	A	A	A
Total	*31*	*19*	*16*	*14*

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[a] Collections by Danglade (1914:37) at the old La Grange lock and dam and at Meredosia.
[b] Collections made in the early 1930's in the vicinity of Meredosia by Dr. J. P. E. Morrison (pers. comm., 4 January 1968).
[c] Collections made 2 miles above Meredosia in 1955 by Dr. Paul W. Parmalee (pers. comm., 21 November 1966).
[d] 1966 survey in the vicinity of Meredosia (river miles 70.8–79.8).
[e] P designates present and A designates absent.

was taken alive by Dr. Parmalee in 1955 (pers. comm., 21 November 1966) from the Alton pool and may still occur there as a rare species. The absence of this species in the 1966-1969 study and the present restricted range and scarcity of the four other species mentioned above, all of which were taken alive at Meredosia by Dr. Morrison in 1930, suggested that pollution affecting mussels probably has slightly increased in this section of the river since 1930.

ORGANOCHLORINE PESTICIDES

The entire bodies (excluding shells) of 14 mussels representing seven species collected from five different locations in the Illinois River during the 1966 survey were analyzed for the presence of organochlorine pesticides (Table 17). All of the mussels analyzed contained residues of these pesticides; however, no measureable peaks were detected in a washboard (*M. gigantea*) collected from

Table 17.—Organochlorine pesticides present in mussels collected from the Illinois River during August 1966.[a]

Kind of Mussel	*River Mile Number Where Mussel Was Taken*	*Pesticides in Parts Per Million*				
		DDT	DDE	Heptachlor Epoxide	Dieldrin	Total
M. gigantea (Washboard)	42.3	. . .	0.0322	0.0135	0.0063	0.0520
” ” ”	106.7	. . .	NMP[b]	NMP	NMP	NMP
A. plicata (Three-Ridge)	42.3	. . .	0.0107	0.0056	. . .	0.0163
” ” ”	106.7	. . .	0.0143	0.0257	0.0143	0.0543
” ” ”	171.8	. . .	0.0275	0.0247	0.0063	0.0585
” ” ”	174.1	0.0281	0.0056	0.0091	0.0094	0.0522
Q. quadrula (Maple-Leaf)	42.3	. . .	0.0089	0.0056	. . .	0.0145
” ” ”	106.7	. . .	0.0071	0.0097	0.0045	0.0213
Q. pustulosa (Pimple-Back)	42.3	. . .	0.0054	0.0021	. . .	0.0075
A. g. corpulenta (Floater)	106.7	. . .	0.0179	0.0139	. . .	0.0318
” ” ” ”	174.1	. . .	0.0303	0.0110	0.0073	0.0486
” ” ” ”	196.1	. . .	0.0066	0.0143	0.0052	0.0261
L. fragilis (Fragile Paper Shell)	106.7	. . .	0.0115	0.0111	0.0054	0.0280
P. alata (Pink Heel-Splitter)	196.1	0.0225	0.0066	0.0169	0.0063	0.0523

[a] Determinations were made by Dr. W. N. Bruce of the Illinois Natural History Survey.
[b] NMP indicates no measurable peak.

the La Grange pool at river mile 106.7. From this same site measurable amounts of these pesticides were found in four other species of mussels (Table 17).

The analysis indicated that considerable variation occurred in the amounts of pesticide residues the mussels contained; however, in no instance did the total concentration exceed 0.0585 ppm, and the average content was 0.0331 ppm. These values may give some insight as to the organochlorine concentrations in the river, since mussels are considered excellent monitors of these pesticides in the freshwater environment (Bedford, Roelfs, & Zabik 1968:125). Because the Illinois River is located in the agricultural belt of the midwest, the amounts of pesticide residues in the mussels analyzed in this study were expected to be much greater than they were. Possibly they were low because some of the pesticides had been adsorbed in the bottom muds of the tributary streams of the Illinois River.

It was not known what effect, if any, organochlorine pesticides have had upon the mussel population of the river. The present trend among Illinois farmers is toward the use of organophosphate pesticides, which are less persistent in the environment than the organochlorine pesticides (Dr. W. N. Bruce, pers. comm., 1 May 1969).

CONSERVATION AND MANAGEMENT

The foregoing analysis indicated that during the past 75 years the Illinois River has changed from an excellent mussel stream to a poor one. The major factors involved in this change have been domestic, industrial, and agricultural pollution. Any environmental improvement for mussel life as well as other aquatic life in the Illinois River can be obtained only through a reduction or more advanced treatment of the wastes being discharged into the river, together with the development and adoption of a new soil conservation plan on the river's watershed to control rapid runoff. These are the basic management needs for the river, and if they are not developed and applied, the environment for aquatic life in much of the Illinois River will continue to deteriorate.

Other management recommendations developed as a result of this study involved the commercial mussel fishery of the river. In 1964 and 1965 a small amount of commercial mussel fishing was done above Beardstown near Browning and Bath. However, in 1966 all mussel fishing was done in the lower 87 miles of the river between Beardstown and its mouth. This was the only known continuous stretch of the river containing a sufficient number of mussel beds large enough to attract commercial clammers in 1966 (Fig. 16). The locations of the beds fished commercially in 1966 are given in Table A-26. In addition, three-ridges occurred abundantly enough in 1966 just below Lower Peoria Lake and in Lower and Middle Peoria lakes to have provided commercial fishing.[1]

Considerable variation existed in the estimates of the standing crops of mussels in the commercial beds sampled with

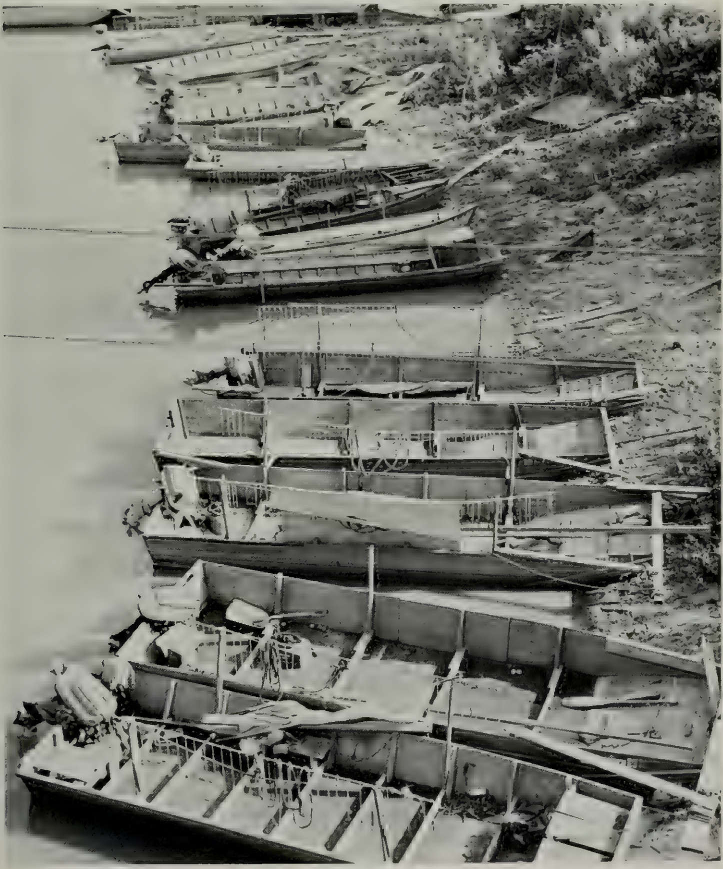

Fig. 16.—Johnboats used by commercial mussel fishermen in the Alton navigation pool of the Illinois River in 1966. Photo by Alvin C. Lopinot.

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[1] Commercial mussel fishermen removed 208,500 pounds of shells from those waters in 1969 (Webb Moss, pers. comm., 30 October 1969).

the dredge in 1966 (Table A-27). These variations were probably the result of sampling errors, differences in the carrying capacities of the beds, and differences in fishing pressure on various beds. The estimates of the standing crops of mussels in two unfished beds in the Peoria pool (river miles 162.3 and 168.2) were thought by the author to give some indication of the number of pounds per acre of commercial-sized mussels (height 2.5 inches or more) that might have been expected in the beds of the lower river in 1966 had they not been fished in recent years. The estimated standing crops of shells of commercial size in these two unfished beds in the Peoria pool were 536 pounds and 2,030 pounds per acre, whereas in the commercially fished beds of the lower river the standing crops of these shells ranged from 51 to 1,312 pounds per acre. These differences in standing crops suggested that many of the beds in the lower river had been heavily fished in recent years.

Additional evidence of heavy fishing pressure in the lower river was reflected by size differences in the three-ridges (*A. plicata*) taken in the survey in the lower river (Alton pool) and the Peoria pool. The three-ridge was the most abundant commercial shell occurring in the river in 1966. In the survey collections in the Alton pool only 39.8 percent of the three-ridges taken (1,598 shells) were of commercial size, whereas in the unfished Peoria pool 64.0 percent of the three-ridges taken (689 shells) were of commercial size. This highly significant difference in the sizes of the three-ridges between the pools was believed to be the result of the selective removal of the large, desirable, commercial-sized shells by commercial clammers. The growth rate of the three-ridge was better in the Peoria pool than it was in the Alton pool, but it was not great enough to account for the differential in commercial-sized shells found in the two pools (Table A-13).

In 1967 and 1968 little commercial mussel fishing was done in the Illinois River because of the lack of a market for the shells. The market for Illinois River shells picked up again in 1969. In the author's opinion, the mussel fishery should be carefully regulated to prevent overfishing. The fishery could be regulated by a Department of Conservation temporary administrative order restricting mussel fishing in the river to a limited period during a year when a market demand for shells was anticipated. In slack years the fishery would regulate itself. Shell buyers should be required to furnish the Department of Conservation with accurate statistics on the numbers of tons purchased by them from Illinois River fishermen. Such statistics would be of value in making annual appraisals of the condition of the mussel fishery.

The Japanese need relatively large, thick shells for the nuclei used in the culturing of pearls. Their buyers wanted only shells having a minimum height of 2.5 inches, and they preferred three-ridges and washboards of 3.0 inches or more in height. As was mentioned earlier, the mussel fishery on the Illinois River in 1966 depended largely upon the abundant three-ridge shell. In this study it was found that in the Illinois River the three-ridge did not attain the height of 2.5 inches until it was 10–12 years of age and that it required 18–20 years to attain a height of 3.0 inches (Table A-13). As a result of this slow growth, very few three-ridges having a height of 3.0 inches or more were found in the river (Table A-12).

The washboard was not nearly as abundant as was the three-ridge, but because of its size, it was the second most important commercial shell occurring in the river (Table 18). In the Illinois River washboards attained a height of 2.5 inches within 7 years and a height of 3.0 inches within 9 years (Table A-11). In the 1966 survey collections 90.3 percent of the washboards taken had a height of 3.0 inches or more (Table A-10). Most of the washboards taken commercially were of the preferred size; however, the bulk of the commercial fishery depended upon three-ridges having a height of 2.5–3.0 inches. Therefore, the adoption of a law requiring that three-ridges taken commercially from Illinois waters have a minimum height of 3.0 inches would virtually eliminate the commercial mussel fishery on the Illinois River.

Table 18.—Species composition of mussel shells in sorted commercial piles along the Illinois River at Meredosia and Kampsville in 1966.

Kind of Mussel	*Number Measured*	*Percent of Shells in Commercial Piles*
Three-Ridge	957	74.8
Washboard	200	15.6
Maple-Leaf	64	5.0
Pimple-Back	28	2.2
Others[a]	30	2.4
Total	*1,279*	*100.0*

[a] Included pig-toe, slough sand-shell, floaters, rock pocketbook, and white heel-splitter (none of these was of any value either because of size or shell thickness and texture).

In 1966 Illinois regulations permitted the taking of rough shells 1.75 inches and smooth shells 3.0 inches or larger in their greatest dimensions. Under these regulations mussel fishermen were permitted to take shells that were too small for use by the pearl-culture industry. The buyers culled out many of the small shells and informed the fishermen that they needed shells having a height of at least 2.5 inches. The sorted piles of shells (Fig. 17) contained a variety of species of mussels living in the Alton pool, some of which had heights of only 1.5 inches. Many of the shells that had been sorted out were of noncommercial

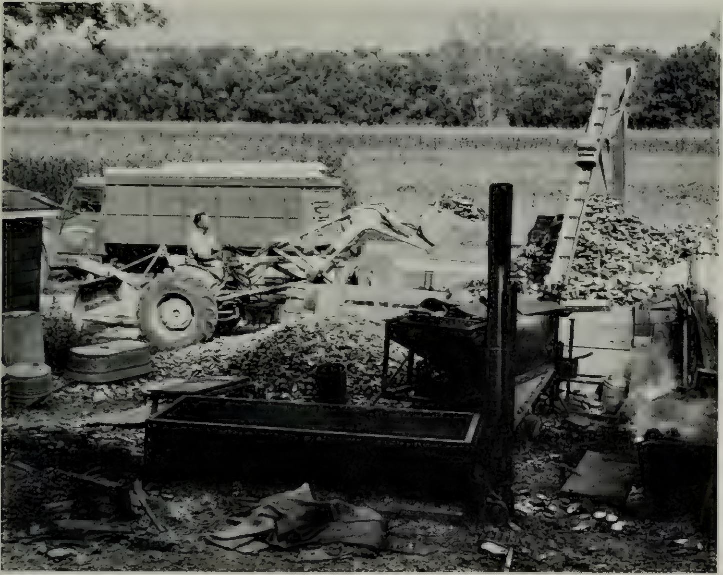

Fig. 17.—A shell buyer's operation in 1966 below Kampsville, Illinois. Most of these shells were three-ridges (**A. plicata**) and washboards (**M. gigantea**) taken by commercial mussel fishermen from the Alton pool of the Illinois River. Photo by Alvin C. Lopinot.

species. In the sorted commercial shell piles examined by us in 1966 few species other than three-ridges and washboards were of commercial sizes (Table 18). In the Illinois River very few maple-leaf and pimple-back shells attained a height of 2.5 inches or more (Tables 18, A-15, and A-16), and as a result, most of these shells taken by clammers were wasted because of their small sizes. In 1967 the Seventy-fifth General Assembly of Illinois passed a law making it unlawful to take mussels in Illinois with shells less than 2.5 inches on the shortest line from the center of the hinge side and at a right angle across the shell to the outer edge (height). The enforcement of this law should reduce the former wanton waste of mussels occurring in the Illinois River.

Other new state regulations on mussel fishing specify the methods and kinds of equipment that commercial clammers may use to take mussels in the Illinois River. These are crowfoot bars, hand picking (wading), hand rakes, hand forks, and hand dredges. Wisely, these regulations prohibited the use of basket dredges, self-contained or ancillary air diving devices, and mechanical or suction devices. Various analyses of the efficiency and selectivity of the methods of mussel fishing employed in the 1966 survey are contained in the appendix of this paper (Tables A-10, A-12, A-15, A-16, A-28, A-29, and A-30). As indicated in these analyses, large numbers of small mussels were taken with the crowfoot bar and hand dredge. No attempt was made to determine the mortality of small mussels caught with the crowfoot bar or dredge and returned to the river. In our collections made by wading, mussels of all sizes were kept. However, commercial clammers using the wading method could be very selective in the sizes of mussels taken.

Conservation and management planners interested in the pearly mussels of the Illinois River should look beyond the mussels' value as a commercial resource and consider that these organisms are an intricate part of the ecosystem of the river. The present study has demonstrated that 25 kinds of mussels already have been extirpated from the river by the effects of man's activities, and if remedial measures are not taken soon, others will also vanish.

SUMMARY

1.—The Illinois River is 272.9 miles long and is formed by the confluence of the Des Plaines and Kankakee rivers southwest of Chicago. It empties into the Mississippi River at Grafton, Illinois. Since 1900 Lake Michigan water has been diverted through the Chicago Sanitary and Ship Canal into the Des Plaines River and thence into the Illinois. Through the years this canal has transported the treated and untreated wastes from the Chicago area into the Illinois River system. These wastes together with those from other cities, industries, and agriculture along the Illinois waterway have drastically affected the biota of the river. There were only minor sources of domestic and industrial pollution along the lower 150 miles of the river. Locks and dams, together with dredging, maintain a 9-foot navigation channel to form the Illinois waterway connecting the Mississippi River with Lake Michigan.

2.—A considerable amount of historical biological and chemical data relative to the Illinois River has been published. These data, together with museum records, furnished the background for the present biological investigation.

3.—In 1966 a survey of the pearly mussels (Unionacea) of the Illinois River was made. In this survey 4,247 live mussels were taken in 429 collections from various parts of the river. These collections were made with an exploratory crowfoot bar, with a dredge, and by wading. The largest estimated standing crop of live mussels found in the river was 6,040 pounds per acre. (Several live mussels were obtained from commercial mussel fishermen operating in the Peoria pool in 1969, and the records of these shells are included in the text.)

4.—Subfossil shell collections were made at 21 locations along the Illinois River in 1966.

5.—Twenty-four kinds of living mussels were taken from the Illinois River and its bottomland lakes in the 1966-1969 period. Five species were represented by single specimens. The three-ridge (*A. plicata*) was the most abundant mussel and made up 62.4 percent of the mussels collected. Mussels which were fairly common were the pimpleback (*Q. pustulosa*), the maple-leaf (*Q. quadrula*), the washboard (*M. gigantea*), and the floater (*A. g. corpulenta*).

6.—At least 49 different kinds of mussels were present in the Illinois River and its adjoining bottomland lakes in the 1870-1900 period. Since that period 25 kinds of mussels apparently have been extirpated from these waters. The distribution of many of the surviving species is now quite limited. Domestic and industrial pollution have been major factors adversely affecting mussel life in the Illinois River. Siltation probably also has affected certain species of mussels, such as the yellow sand-shell (*L. a.* f. *anodontoides*).

7.—At least 38 different kinds of mussels are known to have occurred in the upper river (Starved Rock and Marseilles navigation pools) in the 1870-1900 period. By 1912 pollution had virtually wiped out the mussels in this section, and in the 1966 survey no living mussel was taken there. As a result of waste treatment, the dissolved oxygen content of the upper river was much higher in the mid-1960's than it had been in the 1911-1928 period.

8.—By 1930 pollution had affected in varying degrees the mussel life of the entire river. Pollution has had less effect on mussels in the lower part of the river than it has had in the upper portion; however, even in the lower river 21 kinds of mussels have been extirpated in the past 75 years.

9.—The species of mussels found most tolerant to pollution in the Illinois River were the three-ridge (*A. plicata*), the floater (*A. g. corpulenta*), the slough sand-shell (*L. a.* f. *fallaciosa*), the maple-leaf (*Q. quadrula*), the fragile paper shell (*L. fragilis*), the pink heel-splitter (*P. alata*), and the fragile heel-splitter (*P. laevissima*).

10.—The distance and time required for at least partial dissipation of domestic and industrial pollutants below the Chicago-Joliet and Peoria-Pekin metropolitan areas were reflected by the absence, presence, and abundance of certain species of mussels.

11.—Experimental deletion-type bioassay studies with living mussels and/or other aquatic organisms in river waters and bottom muds might be of value to sanitary and industrial engineers. Such studies might isolate the key pollutants limiting mussels and other aquatic life in a stream, thereby greatly reducing costs in the construction and operation of advanced waste treatment plants.

12.—Comparisons between old and new base-line data for mussels revealed that, in spite of the great reduction since 1922 in the biochemical oxygen demand of the wastes discharged into the Illinois waterway, conditions for mussel life have remained poor in most parts of the river.

13.—It was believed that natural selection has played an important role in reestablishing the mussel beds in Peoria Lake. Improved treatment of municipal and industrial wastes have also undoubtedly helped to improve Peoria Lake as a mussel habitat.

14.—The average amount of organochlorine pesticides in the mussels analyzed from the Illinois River in 1966 was 0.0331 ppm.

15.—Length and height measurements were made of the shells taken alive in the 1966 survey and of some shells in commercial shell piles along the river. Age determinations were made of most of the live mussels taken in the survey.

16.—During the first part of this century the Illinois River supported a large commercial mussel fishery. The effects of pollution on mussel life and the use of plastics for making buttons virtually eliminated this mussel fishing industry. Recently the demand for shells by the Japanese pearl-culture industry has rejuvenated commercial mussel fishing on the Illinois River.

17.—In 1966 a total of 1,118.4 tons of shells were removed from the Illinois River commercially. These shells were valued at $109,460.83. All of the 1966 commercial mussel fishing on the Illinois River was done on its lower 87 miles. The locations of the mussel beds fished commercially in 1966 and estimates of standing crops of many of these beds are included in this paper. In 1969 commercial mussel fishing was resumed in the vicinity of Peoria where 104.3 tons of shells were removed in that year.

18.—The three-ridge (*A. plicata*) comprised 74.8 percent of the shells taken commercially from the Illinois River in 1966. The second most important commercial shell was the washboard (*M. gigantea*).

19.—The three-ridge mussel required 10–12 years to attain the minimum commercial size of 2.5 inches in height in the Illinois River. The washboard attained this height within 7 years. Most of the desirable *Quadrula* species in this river were too small for commercial use.

20.—The survey data indicated that the mussel beds had recently received heavy fishing pressure in the lower river. Conservation and management recommendations for the mussel fishery are suggested in this paper.

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Table A-1.—Ranges and averages of chemical and bacteriological determinations made on the Illinois River in 1966 by the Illinois State Sanitary Water Board (1967).

Analyses	*Alton Pool*	*La Grange Pool*		*Peoria Pool*			*Starved Rock Pool*	*Marseilles Pool*
	71.2[a]	87.9	119.7	161.6	189.2	218.4	239.7	263.5
Hardness ppm								
Range	240–444	240–432	240–444	232–448	216–440	220–416	204–356	212–388
Average	*307*	*301*	*306*	*322*	*320*	*318*	*249*	*293*
Chlorides ppm								
Range	22–72	22–60	18–96	28–68	28–64	24–62	27–58	26–80
Average	*41*	*41*	*46*	*46*	*45*	*44*	*49*	*55*
Sulfate ppm								
Range	20–66	11–49	12–54	19–90	22–98	17–90	. . .	14–123
Average	*33*	*31*	*32*	*36*	*37*	*39*	. . .	*44*
Total Solids ppm								
Range	350–500	340–490	330–540	370–550	330–550	350–540	349–476	360–550
Average	*413*	*413*	*427*	*437*	*439*	*451*	*396*	*458*
BOD ppm								
Range	0–8	1–8	0–8	2–9	3–10	3–10	1–30	3–8
Average	*4*	*5*	*6*	*6*	*6*	*6*	*15*	*6*
Nitrate ppm								
Range	. . .	. . .	. . .	26–26	. . .	. . .	. . .	4–5
Average	. . .	. . .	. . .	*26*	. . .	. . .	. . .	*4*

[a] **River miles, i.e., miles from the mouth of the Illinois River at Grafton, Illinois.**

Table A-1.—Continued

Analyses	*Alton Pool*	*La Grange Pool*		*Peoria Pool*			*Starved Rock Pool*	*Marseilles Pool*
	71.2[a]	87.9	119.7	161.6	189.2	218.4	239.7	263.5
Radioactivity								
Alpha picocurie Per liter								
Range	0–12	0–8	0–9	0–5	0–4	2–6	0–1	1–5
Average	*3*	*2*	*3*	*3*	*2*	*2*	*0*	*3*
Beta picocurie Per liter								
Range	0–23	0–43	0–32	0–49	0–25	0–25	4–20	0–29
Average	*7*	*12*	*12*	*17*	*11*	*10*	*9*	*14*
Bacterial Counts								
Coliform Per 100 ml								
Range	210–35,000	110–34,000	920–76,000	10–10,000	40–52,000	340–80,000	900–300,000	260–44,000
Average	*9,872*	*13,675*	*25,743*	*1,690*	*6;302*	*17,840*	*49,222*	*11,634*
Enterococcus Per 100 ml								
Range	6–33,000	2–17,000	6–16,000	2–4,200	2–1,300	4–4,000	0–7,000	2–260
Average	*2,900*	*1,497*	*1,539*	*413*	*137*	*644*	*1,244*	*54*
Standard Plate Count Per ml								
Range	1,700–160,000	2,400–78,000	2,100–440,000	1,300–370,000	1,500–35,000	2,300–190,000	7,300–1,500,000	8,100–590,000
Average	*25,050*	*25,475*	*67,641*	*38,858*	*11,033*	*41,218*	*158,665*	*143,918*

Table A-2.—Dissolved oxygen, total alkalinity (methyl orange), pH, temperature, and ABS (detergent) determinations made in the Illinois River channel in July and August 1966.

River Mile[a]	*Dissolved Oxygen in ppm*[b]	*Alkalinity in ppm*	*pH*	*Temperature in Degrees Centigrade*[b]	*ABS (Detergent) in ppm*
		Alton Pool			
26.0	2.3–2.6	...	7.7	26.8	0.05
28.9	1.8–2.1	127	7.6	26.8	0.05
31.5	2.3	...	...	26.8	...
34.2	2.3	127	7.6	26.8	0.1
36.3	2.1	...	...	26.8	...
39.3	1.9–2.0	131	7.7	26.8	0.1
41.4	2.1	...	...	26.8	...
42.8	2.1–2.2	...	7.6	26.8	...
44.9	2.2	...	...	26.7	...
46.1	2.0–2.3	...	7.6	26.8	0.1
50.0	2.7	135	7.6	26.8	0.1
52.7	2.7	...	...	26.8	...
54.8	2.6–2.7	...	7.6	26.8	...
56.4	...	...	...	26.5	0.1
57.8	2.8	...	...	26.6	...
60.8	2.9	...	...	26.4	...
62.6	3.0	135	7.7	26.2	0.1
64.4	3.1	...	...	26.2	...
66.6	3.2	135	7.7	26.4	0.1
68.4	3.3	...	...	26.4	...
69.4	3.3–3.4	...	7.7	26.4	...
71.2	3.3	...	...	26.4	...
73.0	3.4	143	7.7	26.4	0.1
74.5	3.4	...	...	26.6	...
75.9	3.5–3.7	...	...	26.7	...
76.9	3.6	...	7.7	26.7	...
78.4	3.7	...	...	26.7	...
79.3	3.6	143	7.7	26.7	0.1

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[a] Number of miles from mouth of Illinois River at Grafton, Illinois.
[b] Samples taken at 3 feet below the surface.

Table A-2.—Continued

River Mile[a]	*Dissolved Oxygen in ppm*[b]	*Alkalinity in ppm*	*pH*	*Temperature in Degrees Centigrade*[b]	*ABS (Detergent) in ppm*
		La Grange Pool			
81.0	1.1–1.6	147	7.5	26.8	0.1
82.3	1.6	...	...	26.7	...
84.1	1.3–1.9	...	7.6	26.7	...
85.5	1.0–1.6	...	...	26.7	...
87.0	0.9–1.5	147	7.5	26.3	0.1
89.2	0.9	...	...	26.5	...
90.2	0.9–1.0	139	7.4	26.6	0.1
91.5	0.8	...	7.3	26.5	...
94.3	0.8	...	7.3	26.6	...
95.3	0.8–0.9	...	...	26.6	...
97.3	0.8	...	7.3	26.5	...
98.2	0.9–1.1	...	...	26.4	...
99.5	0.9	143	7.3	26.4	0.1
100.9	0.8	...	...	26.4	...
103.4	0.7–0.8	...	7.4	26.7	...
105.5	0.7	...	...	26.8	...
106.9	0.6	143	7.4	26.8	0.1
110.2	0.6–0.7	...	...	26.7	...
113.3	0.6–0.7	...	7.3	26.6	...
114.3	0.5–0.6	...	...	26.6	...
116.3	0.8	...	7.3	26.6	...
117.6	0.9–1.0	...	...	26.4	...
119.7	1.0	143	7.3	26.6	0.1
120.0	1.0	...	...	26.7	...
121.1	0.9–1.0	143	7.4	26.8	0.1
122.8	1.0–1.2	...	7.4	26.6	...
123.6	1.2	...	...	26.8	...
125.8	1.3–1.5	150	7.4	26.3–26.4	0.1
128.0	1.5–1.6	...	...	26.8	...
129.5	1.4	...	7.4	26.6	...
132.0	1.7–1.8	...	...	26.6–26.8	...
134.0	1.5	154	7.4	26.4	0.1
135.7	1.5	...	7.4	26.3	...
139.0	1.6	...	...	26.4	...
140.8	1.9	147	7.4	26.6	0.1
143.2	2.3–2.4	...	7.4	26.7	...
145.5	2.9	143	7.4	26.5	0.1
147.3	2.7	...	...	26.6	...
148.5	3.4	...	7.4	26.5	...
149.4	3.5	...	...	26.3	...
151.2	4.3	147	7.5	26.3	0.1
152.0	4.6–4.7	...	...	26.3	...
153.5	4.7	150	...	26.6	0.1
154.9	5.4–5.5	...	...	26.3	...
156.5	5.8–6.0	...	...	26.5–26.7	...
157.1	5.8	143	7.5	26.7	0.1

Table A-2.—Continued

River Mile[a]	*Dissolved Oxygen in ppm*[b]	*Alkalinity in ppm*	*pH*	*Temperature in Degrees Centigrade*[b]	*ABS (Detergent) in ppm*
Peoria Pool					
159.4	1.5–1.9	154	7.7	28.6–28.8	0.1
161.1	2.2–2.3	...	...	28.9	...
162.4	2.3–4.7	...	8.0	28.7–28.8	...
164.4	2.2–4.7	150	8.3	28.0–28.8	0.1
165.3	2.6–2.9	...	...	28.2–28.4	...
166.8	3.1–4.1	154	7.7	28.3–28.6	0.1
168.9	2.5–5.4	...	...	28.3–29.3	...
170.9	2.1–4.2	...	8.4	29.0–29.3	...
173.4	2.1–5.9	143	8.7	28.8–29.3	0.1
174.9	2.0–3.3	...	7.6	29.1–29.4	...
176.6	1.2	...	7.5	28.9	...
177.4	0.9–1.1	...	...	29.0	...
179.0	0.9–1.0	147	7.4	29.1	0.1
179.7	0.9	...	...	29.1	...
181.0	0.9	...	...	29.2	...
181.3	0.9	147	7.4	29.2	0.1
182.8	0.9	...	7.3	29.5	...
184.1	1.1	...	...	29.4–29.5	...
186.4	0.9–1.1	147	7.3	29.6–29.7	...
189.0	1.0	...	...	29.8	...
190.0	0.9	143	7.3	29.8	0.2
191.6	1.2	...	7.3	29.8	...
193.3	1.1	...	...	29.8	...
195.8	1.0–1.2	143	7.2	29.8–29.9	0.2
196.2	1.2	147	7.4	29.2	0.1
197.2	1.2	...	...	29.7	...
198.1	1.3–1.4	147	7.4	29.7	...
199.3	1.6	...	7.4	29.7	...
200.4	1.6–1.7	...	...	29.7	...
201.0	1.9	150	7.3	29.8	0.2
202.9	2.2	...	...	29.9	...
204.0	2.3	...	...	30.0	...
205.0	2.4	154	7.4	30.0	0.2
207.6	2.3	...	7.4	29.8	...
209.4	2.1–2.2	...	...	29.8	...
210.7	2.3–2.5	150	7.4	30.0–30.3	0.2
213.4	3.0	...	7.4	29.8	...
214.9	3.3	...	7.4	29.8	...
217.1	3.1	...	...	29.9	...
219.1	3.1–3.2	143	7.4	29.9	0.2
220.7	3.3	...	...	29.9	...
223.9	3.8	...	7.4	29.9	...
225.8	4.5	...	...	30.0	...
226.3	4.7–4.8	...	7.4	30.0	...
228.1	5.0	...	...	30.0	...
229.7	5.3	158	7.4	30.0	0.2

Table A-2.—Continued

River Mile[a]	*Dissolved Oxygen in ppm*[b]	*Alkalinity in ppm*	*pH*	*Temperature in Degrees Centigrade*[b]	*ABS (Detergent) in ppm*
Starved Rock Pool					
231.7	6.6–9.1	143	7.8	27.8–28.3	0.1
233.0	6.3–6.4	...	7.9	28.1–29.3	...
234.5	8.4–8.9	...	8.1	28.3–28.6	...
237.2	5.9–6.1	143	7.7	29.0	0.2
238.5	4.7–5.4	...	7.6	28.8	...
239.9	4.4–4.6	...	...	28.8	...
240.6	4.7	143	7.5	29.0	0.1
241.5	5.2	...	7.4	29.1	...
242.9	5.1	...	...	29.3	...
244.1	4.9–5.8	143	7.3	29.1	0.2
Marseilles Pool					
248.2	6.2–6.4	130	7.8	29.1	0.1
249.4	5.4	...	...	29.3	...
251.0	5.0–5.8	...	7.5	29.3	...
251.8	4.9	...	7.7	29.3	...
253.0	5.1–5.8	...	...	29.8	...
253.6	5.0	...	7.7	29.8	...
255.0	4.9–5.1	...	...	29.6	...
256.0	4.4	147	7.5	29.8	0.2
257.6	4.2	...	...	29.8	...
258.8	3.5	...	...	29.8	...
259.3	3.5	...	7.3	29.8	...
260.7	3.0–3.2	...	...	29.8	...
261.0	3.0–3.2	...	...	29.8	...
262.3	2.8–2.9	...	7.3	29.8	...
263.7	3.0–3.3	150	7.3	29.8	0.2
265.0	3.3	...	7.3	29.8	...
265.8	3.7	...	...	30.0	...
266.4	3.8	...	...	30.3	...
267.2	3.9–4.0	...	7.3	30.6	...
269.5	4.2–4.4	...	...	31.0	...
270.6	4.7–4.8	155	7.3	31.0–31.3	0.2
Dresden Pool					
272.1	0.9–1.0	162	7.4	31.0	0.4

Table A-3.—Numbers and kinds of live mussels taken during the 1966 survey of the Illinois River, by navigation pool and river section.

Species	*Alton Pool*									*La Grange Pool*										
	River Mile[a] or Bottomland Lake[b]								Total From Alton Pool	River Mile or Bottomland Lake										Total From La Grange Pool
	0.9 to 5.5	10.5 to 15.1	19.2 to 29.0	30.5 to 39.2	40.3 to 48.3	51.0 to 58.9	60.8 to 69.4	70.8 to 79.8		80.3 to 87.9	90.2 to 100.5	106.6 to 114.0	Bath Chute	Lake Matanzas	115.3 to 123.0	Quiver Lake	125.0 to 135.5	140.5 to 149.7	150.6 to 156.6	
Fusconaia ebena	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fusconaia f. f. undata	1	3	3	0	1	3	1	14	26	0	0	0	0	0	0	0	0	0	1	1
Megalonaias gigantea	31	6	30	21	20	47	24	4	183	5	2	7	7	0	0	2	0	0	0	23
Amblema plicata	177	124	133	100	235	226	432	171	1,598	37	82	140	15	0	25	49	5	3	7	363
Quadrula quadrula	29	11	7	22	39	29	94	36	267	10	17	21	6	0	13	3	8	0	8	86
Quadrula pustulosa	12	18	13	23	94	67	154	32	413	0	1	8	1	0	0	3	0	0	0	13
Quadrula nodulata	6	3	1	6	7	1	25	14	63	3	2	0	0	0	0	0	0	0	0	5
Arcidens confragosus	1	20	4	4	9	15	4	1	58	5	0	4	2	0	1	0	4	0	0	16
Lasmigona complanata	0	1	0	0	0	0	2	0	3	0	0	1	0	0	1	0	1	2	0	5
Anodonta g. grandis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
Anodonta g. corpulenta	18	3	1	1	0	1	12	2	38	1	0	3	1	0	2	0	10	9	1	27
Anodonta imbecillis	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	2	0	0	2
Anodonta suborbiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Obliquaria reflexa	20	4	3	0	3	5	5	8	48	0	0	0	0	0	0	1	0	0	0	1
Obovaria olivaria	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Truncilla truncata	3	0	0	0	0	0	1	4	8	0	1	1	0	0	0	0	0	0	0	2
Truncilla donaciformis	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Leptodea fragilis	2	3	1	0	2	5	14	10	37	0	7	7	1	0	4	0	0	1	1	21
Proptera alata	3	2	0	0	1	2	1	1	10	0	0	0	0	0	0	0	0	0	1	1
Proptera laevissima	13	2	0	0	2	0	2	1	20	1	0	1	0	0	0	0	5	4	1	12
Carunculina parva	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lampsilis a. f. fallaciosa	7	1	0	0	1	4	4	12	29	5	2	0	0	0	0	0	1	0	0	8
Lampsilis r. luteola	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2
Total	*326*	*201*	*196*	*178*	*414*	*405*	*777*	*310*	*2,807*	*67*	*115*	*193*	*34*	*1*	*46*	*60*	*36*	*19*	*20*	*591*

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[a] Miles from the mouth of the Illinois River at Grafton, Illinois.
[b] Meredosia Lake was fished for mussels, but none was taken there.

Table A-3.—Continued

Species	*Peoria Pool*												*Starved Rock Pool*	*Marseilles Pool*	*Total*
	River Mile											Total From Peoria Pool			
	158.1 to 160.0	161.1 to 162.3[c]	163.0 to 166.1[d]	166.3 to 166.6[d]	167.2 to 174.9[d]	174.9 to 179.7	180.5 to 188.0	190.0 to 199.3	200.4 to 209.4	210.7 to 219.8	220.7 to 229.3				
Fusconaia ebena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fusconaia f. f. undata	0	7	0	2	10	0	0	0	0	0	0	19	0	0	46
Megalonaias gigantea	0	0	0	0	0	0	0	1	0	0	0	1	0	0	207
Amblema plicata	1	185	24	16	454	0	5	2	1	0	1	689	0	0	2,650
Quadrula quadrula	0	16	0	1	19	0	0	0	0	1	0	37	0	0	390
Quadrula pustulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	425
Quadrula nodulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66
Arcidens confragosus	0	0	0	0	1	0	0	0	0	0	0	1	0	0	78
Lasmigona complanata	0	1	1	0	3	0	0	0	0	0	0	5	0	0	13
Anodonta g. grandis	0	0	0	0	1	0	0	1	0	0	0	2	0	0	4
Anodonta g. corpulenta	0	4	2	2	34	2	0	6	0	0	1	51	0	0	116
Anodonta imbecillis	0	0	0	0	0	0	0	1	0	0	0	1	0	0	5
Anodonta suborbiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Obliquaria reflexa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49
Obovaria olivaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Truncilla truncata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Truncilla donaciformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Leptodea fragilis	1	0	0	1	1	0	0	1	0	0	2	6	0	0	64
Proptera alata	1	1	0	0	0	0	0	3	0	0	0	5	0	0	16
Proptera laevissima	0	3	2	1	1	2	0	1	0	0	0	10	0	0	42
Carunculina parva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lampsilis a. f. fallaciosa	0	0	2	1	6	2	1	2	0	0	2	16	0	0	53
Lampsilis r. luteola	0	0	0	3	3	0	0	0	0	0	0	6	0	0	8
Total	*3*	*217*	*31*	*27*	*533*	*6*	*6*	*18*	*1*	*1*	*6*	*849*	*0*	*0*	*4,247*

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[c] From this section of the river in 1969 these additional kinds of mussels were collected: *Megalonaias gigantea, Quadrula pustulosa, Tritogonia verrucosa,* and *Lampsilis r. luteola.*

[d] From these sections of the river in 1969 commercial mussel fishermen took a few living *Megalonaias gigantea* specimens.

Table A-4.—Numbers of collections and time expended in fishing for mussels by three methods in the Alton navigation pool of the Illinois River in the 1966 survey.

River Mile	*Crowfoot Bar*		*Dredge*		*Wading*	
	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Hours
0.9– 5.5	6	30:48	2	4:28	1	1.5
10.5–15.1	9	89:36	2	4:22	1	1.5
19.2–29.0	13	116:20	3	5:49	0	. . .
30.5–39.2	12	115:38	3	6:41	0	. . .
40.3–48.3	12	110:26	3	6:29	1	1.0
51.0–58.9	21	148:27	6	7:38	0	. . .
60.8–69.4	21	213:59	8	9:33	1	5.0
Meredosia Lake	5	92:04	2	13:31	0	. . .
70.8–79.8	14	109:15	1	0:50	1	3.0
Total	*113*	*1,026:33*	*30*	*59:21*	*5*	*12.0*

Table A-5.—Numbers of collections and time expended in fishing for mussels by three methods in the La Grange navigation pool of the Illinois River in the 1966 survey.

River Mile	*Crowfoot Bar*		*Dredge*		*Wading*	
	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Hours
80.3– 87.9	6	53:40	1	2:25	3	2.75
90.2–100.5	19	202:07	4	13:49	0	. . . .
106.6–114.0	14	176:49	4	7:26	1	2.00
Bath Chute	6	78:03	3	7:29	0	. . . .
Lake Matanzas	2	71:20	2	14:37	1	1.00
115.3–123.0	13	185:02	3	4:52	1	1.50
Quiver Lake	1	46:22	2	10:28	1	1.50
125.0–135.5	13	197:38	2	5:35	2	3.50
140.5–149.7	14	175:20	2	2:44	1	0.50
150.6–156.6	8	128:39	1	1:06	0	. . . .
Total	*96*	*1,315:00*	*24*	*70:31*	*10*	*12.75*

Table A-6.—Numbers of collections and time expended in fishing for mussels by three methods in the Peoria navigation pool of the Illinois River in the 1966 survey.

River Mile	*Crowfoot Bar*		*Dredge*		*Wading*	
	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Hours
158.1–160.0	3	83:06	0	...	0	...
161.1–162.3	7	45:55	3	3:07	0	...
163.0–166.1	5	135:35	4	93:58	0	...
166.3–166.6	1	31:26	0	...	1	1.5
167.2–174.9	18	447:37	9	76:58	5	7.5
174.9–179.7	4	136:13	1	17:41	1	1.5
180.5–188.0	10	151:00	1	1:06	3	4.0
190.0–199.3	12	181:33	1	1:08	3	3.5
200.4–209.4	8	158:33	0	...	2	3.0
210.7–219.8	8	130:50	0	...	1	0.5
220.7–229.3	7	121:44	1	0:44	0	...
Total	*83*	*1,623:32*	*20*	*194:42*	*16*	*21.5*

Table A-7.—Numbers of collections and time expended in fishing for mussels by three methods in the Starved Rock navigation pool of the Illinois River in the 1966 survey.

River Mile	*Crowfoot Bar*		*Dredge*		*Wading*	
	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Hours
233.7–236.5	5	77:26	0	..	1	0.25
239.0–244.3	7	73:07	0	..	0	....
Total	*12*	*150:33*	*0*	..	*1*	*0.25*

Table A-8.—Numbers of collections and time expended in fishing for mussels by three methods in the Marseilles navigation pool of the Illinois River in the 1966 survey.

River Mile	*Crowfoot Bar*		*Dredge*		*Wading*	
	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Minutes and Seconds	Number of Collections	Time Used in Hours
249.2–259.0	11	139:09	0	..	0	...
260.2–272.0	7	104:56	0	..	1	1.5
Total	*18*	*244:05*	*0*	..	*1*	*1.5*

Table A-9.—Average observed lengths and heights of pig-toes (**Fusconaia flava** f. **undata**) of various ages from the 1966 Illinois River collections.

Age in Years	*Average Length in Inches*	*Average Height in Inches*	*Number of Mussels*
5	2.1	1.6	1
6	2.3	1.8	1
7	2.0	1.6	4
8	2.1	1.7	6
9	2.3	1.9	10
10	2.6	2.1	7
11	2.6	1.9	7
12	2.7	2.2	4
13	2.9	2.4	1
14	2.8	2.3	2
15	..	..	0
16	2.8	2.4	2
17	2.5	2.0	1
Total	..	..	*46*

Table A-10.—Height frequency distribution of washboards (**Megalonaias gigantea**) taken from the Illinois River by crowfoot bar, dredge, and wading in the 1966 survey.

Height in Inches	*Crowfoot Bar*		*Dredge*		*Wading*		*Total*	
	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch
2.1	2	1.4	0	0.0	0	0.0	2	1.0
2.2	1	0.7	0	0.0	0	0.0	1	0.5
2.3	0	0.0	1	2.7	0	0.0	1	0.5
2.4	1	0.7	0	0.0	0	0.0	1	0.5
2.5	0	0.0	2	5.4	0	0.0	2	1.0
2.6	3	2.1	0	0.0	0	0.0	3	1.4
2.7	2	1.4	0	0.0	0	0.0	2	1.0
2.8	2	1.4	0	0.0	0	0.0	2	1.0
2.9	5	3.5	1	2.7	0	0.0	6	2.9
3.0	6	4.2	1	2.7	1	3.9	8	3.9
3.1	4	2.8	1	2.7	3	11.5	8	3.9
3.2	6	4.2	0	0.0	4	15.4	10	4.8
3.3	6	4.2	2	5.4	1	3.9	9	4.3
3.4	11	7.6	3	8.1	1	3.9	15	7.3
3.5	17	11.8	3	8.1	1	3.9	21	10.1
3.6	11	7.6	2	5.4	3	11.5	16	7.7
3.7	11	7.6	4	10.9	2	7.7	17	8.2
3.8	11	7.6	2	5.4	4	15.4	17	8.2
3.9	13	9.0	1	2.7	0	0.0	14	6.8
4.0	7	4.9	3	8.1	1	3.8	11	5.3
4.1	8	5.5	1	2.7	0	0.0	9	4.3
4.2	11	7.6	4	10.8	1	3.8	16	7.7
4.3	3	2.1	0	0.0	2	7.7	5	2.4
4.4	0	0.0	3	8.1	0	0.0	3	1.4
4.5	2	1.4	3	8.1	1	3.8	6	2.9
4.6	1	0.7	0	0.0	0	0.0	1	0.5
4.7	0	0.0	0	0.0	1	3.8	1	0.5
Total	*144*	*100.0*	*37*	*100.0*	*26*	*100.0*	*207*	*100.0*

Table A-11.—Average observed lengths and heights of washboards (**Megalonaias gigantea**) of various ages from the 1966 Illinois River collections.

Age in Years	*Alton Pool*			*Above La Grange Dam*			*Entire River*		
	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels
5	3.3	2.1	1	3.7	2.5	1	3.5	2.3	2
6	3.5	2.4	2	...	...	0	3.5	2.4	2
7	3.8	2.5	4	...	...	0	3.8	2.5	4
8	4.3	2.7	5	...	...	0	4.3	2.7	5
9	4.6	3.0	8	...	...	0	4.6	3.0	8
10	4.8	3.2	7	5.7	3.8	1	4.9	3.3	8
11	5.0	3.3	22	5.8	3.6	3	5.1	3.3	25
12	5.2	3.4	23	5.5	3.6	2	5.2	3.4	25
13	5.2	3.4	17	5.9	3.8	3	5.3	3.4	20
14	5.7	3.7	13	6.1	4.0	2	5.8	3.7	15
15	5.6	3.7	18	6.5	4.2	4	5.8	3.8	22
16	6.0	3.8	17	6.4	4.2	2	6.1	3.9	19
17	6.1	3.9	5	6.7	4.3	3	6.4	4.1	8
18	6.3	4.2	11	6.8	4.4	1	6.4	4.2	12
19	6.3	4.0	5	...	...	0	6.3	4.0	5
20	6.4	4.2	9	7.2	4.5	1	6.5	4.2	10
21	6.4	4.0	5	...	...	0	6.4	4.0	5
22	6.5	4.2	4	...	...	0	6.5	4.2	4
23	6.5	4.2	2	...	...	0	6.5	4.2	2
24	6.7	4.2	3	...	...	0	6.7	4.2	3
25	6.7	4.3	2	...	...	0	6.7	4.3	2
26	...	...	0	6.6	4.0	1	6.6	4.0	1
Total	...	...	*183*	...	...	*24*	...	...	*207*

Table A-12.—Height frequency distribution of three-ridges (**Amblema plicata**) taken from the Illinois River by crowfoot bar, dredge, and wading in the 1966 survey.

Height in Inches	*Crowfoot Bar*		*Dredge*		*Wading*		*Total*	
	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch
1.1	0	0.0	2	0.4	0	0.0	2	0.1
1.2	1	0.1	1	0.2	1	0.1	3	0.1
1.3	1	0.1	6	1.1	1	0.1	8	0.3
1.4	4	0.3	2	0.4	3	0.4	9	0.3
1.5	5	0.4	3	0.5	3	0.4	11	0.4
1.6	6	0.5	2	0.4	9	1.2	17	0.7
1.7	26	1.9	11	2.0	14	1.9	51	1.9
1.8	42	3.1	10	1.8	22	3.0	74	2.8
1.9	54	4.0	22	4.0	23	3.1	99	3.7
2.0	72	5.3	27	4.9	49	6.6	148	5.6
2.1	86	6.3	36	6.6	48	6.5	170	6.4
2.2	117	8.6	43	7.8	68	9.1	228	8.6
2.3	153	11.3	50	9.1	43	5.8	246	9.3
2.4	140	10.3	48	8.7	55	7.4	243	9.2
2.5	145	10.7	58	10.6	52	7.0	255	9.6
2.6	142	10.5	61	11.1	79	10.6	282	10.7
2.7	111	8.2	58	10.5	70	9.4	239	9.0
2.8	105	7.7	38	6.9	65	8.7	208	7.9
2.9	68	5.0	31	5.6	51	6.8	150	5.7
3.0	33	2.4	21	3.8	47	6.3	101	3.8
3.1	26	1.9	12	2.2	26	3.5	64	2.4
3.2	8	0.6	3	0.5	11	1.5	22	0.8
3.3	7	0.5	5	0.9	4	0.5	16	0.6
3.4	1	0.1	0	0.0	1	0.1	2	0.1
3.5	0	0.0	0	0.0	0	0.0	0	0.0
3.6	0	0.0	0	0.0	0	0.0	0	0.0
3.7	1	0.1	0	0.0	0	0.0	1	...[a]
3.8	0	0.0	0	0.0	0	0.0	0	0.0
3.9	1	0.1	0	0.0	0	0.0	1	...[a]
Total	*1,355*	*100.0*	*550*	*100.0*	*745*	*100.0*	*2,650*	*100.0*

[a] Less than 0.1 percent.

Table A-13.—Average observed lengths and heights of three-ridges (**Amblema plicata**) of various ages from the 1966 Illinois River collections.

Age in Years	*Alton Pool*			*La Grange Pool*			*Peoria Pool*			*Entire River*		
	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels
4	1.7	1.3	4	1.9	1.4	2	1.9	1.4	1	1.8	1.3	7
5	2.2	1.6	9	2.4	1.7	2	2.5	1.7	8	2.3	1.6	19
6	2.4	1.7	45	2.4	1.7	8	2.8	2.0	31	2.6	1.8	84
7	2.7	1.9	126	3.0	2.0	22	3.1	2.2	68	2.8	2.0	216
8	3.0	2.1	166	3.0	2.1	27	3.3	2.3	94	3.1	2.2	287
9	3.1	2.2	180	3.4	2.4	21	3.5	2.4	84	3.2	2.3	285
10	3.2	2.3	270	3.6	2.6	27	3.6	2.5	77	3.3	2.4	374
11	3.4	2.4	247	3.7	2.6	38	3.8	2.7	67	3.5	2.5	352
12	3.5	2.5	215	3.8	2.6	43	4.0	2.8	60	3.6	2.6	318
13	3.7	2.6	135	3.9	2.7	44	3.9	2.8	48	3.8	2.6	227
14	3.9	2.7	85	4.1	2.9	38	4.0	2.8	35	4.0	2.8	158
15	4.0	2.8	46	4.2	2.8	27	4.2	2.9	28	4.1	2.8	101
16	4.2	2.9	35	4.4	3.0	23	4.1	2.9	23	4.2	2.9	81
17	4.2	2.9	19	4.3	2.9	15	4.2	2.9	13	4.2	2.9	47
18	4.2	2.9	6	4.4	3.0	14	4.3	2.9	21	4.3	3.0	41
19	4.3	2.9	3	4.9	3.4	2	4.4	3.0	12	4.4	3.0	17
20	4.3	3.0	4	4.3	3.1	6	4.3	3.0	15	4.3	3.0	25
21	4.4	3.0	2	4.7	3.1	2	4.5	3.2	1	4.5	3.0	5
22	. . .	. . .	0	4.8	3.2	2	4.8	3.2	1	4.8	3.2	3
23	4.0	2.9	1	. . .	. . .	0	4.9	3.2	1	4.5	3.1	2
24	. . .	. . .	0	. . .	. . .	0	. . .	. . .	0	. . .	. . .	0
25	. . .	. . .	0	. . .	. . .	0	4.4	3.1	1	4.4	3.1	1
Total	. . .	. . .	*1,598*	. . .	. . .	*363*	. . .	. . .	*689*	. . .	. . .	*2,650*

Table A-14.—Average observed lengths and heights of maple-leafs (**Quadrula quadrula**) of various ages from the 1966 Illinois River collections.

Age in Years	*Alton Pool*			*La Grange Pool*			*Peoria Pool*			*Entire River*		
	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels	Average Length in Inches	Average Height in Inches	Number of Mussels
4	1.6	1.3	6	...	...	0	2.0	1.6	1	1.7	1.3	7
5	1.8	1.4	3	...	...	0	...	...	0	1.8	1.4	3
6	2.0	1.6	12	1.9	1.5	1	2.9	2.1	2	2.1	1.6	15
7	2.1	1.7	17	2.7	2.1	1	2.8	2.1	7	2.3	1.8	25
8	2.2	1.8	33	2.5	2.0	7	3.0	2.2	4	2.3	1.9	44
9	2.3	1.9	42	2.6	2.1	13	3.2	2.4	6	2.5	2.0	61
10	2.5	2.0	43	2.8	2.2	13	3.2	2.4	6	2.6	2.1	62
11	2.5	2.0	42	2.9	2.2	14	3.2	2.5	6	2.7	2.1	62
12	2.6	2.1	35	2.9	2.3	15	3.4	2.5	4	2.8	2.2	54
13	2.8	2.2	20	3.1	2.4	11	...	...	0	2.9	2.3	31
14	2.9	2.3	10	3.1	2.4	5	3.0	2.4	1	2.9	2.4	16
15	2.8	2.4	2	3.6	2.5	3	...	...	0	3.3	2.5	5
16	3.1	2.5	1	3.7	2.8	2	...	...	0	3.5	2.7	3
17	3.2	2.5	1	3.4	2.6	1	...	...	0	3.3	2.6	2
Total	...	...	*267*	...	...	*86*	...	...	*37*	...	...	*390*

Table A-15.—Height frequency distribution of maple-leafs (**Quadrula quadrula**) taken from the Illinois River by crowfoot bar, dredge, and wading in the 1966 survey.

Height in Inches	*Crowfoot Bar*		*Dredge*		*Wading*		*Total*	
	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch
0.9	1	0.4	0	0.0	0	0.0	1	0.2
1.0	0	0.0	0	0.0	0	0.0	0	0.0
1.1	1	0.4	1	0.9	0	0.0	2	0.5
1.2	2	0.9	1	0.9	0	0.0	3	0.8
1.3	2	0.9	1	0.9	0	0.0	3	0.8
1.4	4	1.7	1	0.9	0	0.0	5	1.3
1.5	5	2.1	4	3.8	2	4.1	11	2.8
1.6	12	5.1	4	3.8	3	6.1	19	4.9
1.7	12	5.1	7	6.5	4	8.2	23	5.9
1.8	17	7.3	5	4.7	1	2.1	23	5.9
1.9	26	11.1	11	10.3	6	12.2	43	11.0
2.0	29	12.4	12	11.2	6	12.2	47	12.1
2.1	37	15.8	21	19.6	8	16.3	66	16.9
2.2	32	13.7	11	10.3	4	8.2	47	12.1
2.3	18	7.7	9	8.4	7	14.3	34	8.7
2.4	16	6.8	8	7.5	5	10.2	29	7.4
2.5	13	5.6	4	3.7	3	6.1	20	5.1
2.6	5	2.1	3	2.8	0	0.0	8	2.1
2.7	0	0.0	2	1.9	0	0.0	2	0.5
2.8	2	0.9	2	1.9	0	0.0	4	1.0
Total	*234*	*100.0*	*107*	*100.0*	*49*	*100.0*	*390*	*100.0*

Table A-16.—Height frequency distribution of pimple-backs (**Quadrula pustulosa**) taken from the Illinois River by crowfoot bar, dredge, and wading in the 1966 survey.

Height in Inches	*Crowfoot Bar*		*Dredge*		*Wading*		*Total*	
	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch	Number Caught	Percent of Catch
1.0	7	2.4	3	4.3	0	0.0	10	2.3
1.1	5	1.7	0	0.0	0	0.0	5	1.2
1.2	5	1.7	0	0.0	0	0.0	5	1.2
1.3	15	5.1	5	7.1	1	1.6	21	4.9
1.4	14	4.8	0	0.0	2	3.2	16	3.8
1.5	13	4.4	2	2.9	2	3.2	17	4.0
1.6	41	13.9	8	11.4	9	14.5	58	13.6
1.7	50	17.0	19	27.1	11	17.8	80	18.8
1.8	60	20.4	7	10.0	14	22.6	81	19.0
1.9	25	8.5	17	24.3	6	9.7	48	11.3
2.0	24	8.2	6	8.6	8	12.9	38	8.9
2.1	15	5.1	2	2.9	2	3.2	19	4.5
2.2	12	4.1	1	1.4	5	8.1	18	4.2
2.3	2	0.7	0	0.0	1	1.6	3	0.7
2.4	6	2.0	0	0.0	1	1.6	7	1.6
Total	*294*	*100.0*	*70*	*100.0*	*62*	*100.0*	*426*	*100.0*

Table A-17.—Average observed lengths and heights of pimple-backs (**Quadrula pustulosa**) of various ages from the 1966 Illinois River collections.

Age in Years	*Average Length in Inches*	*Average Height in Inches*	*Number of Mussels*
4	1.3	1.1	4
5	1.4	1.2	8
6	1.6	1.3	24
7	1.8	1.6	53
8	1.9	1.7	83
9	2.0	1.8	97
10	2.1	1.8	63
11	2.2	1.9	45
12	2.3	2.0	22
13	2.5	2.2	12
14	2.4	1.9	7
15	2.5	2.1	5
16	2.5	2.1	3
Total	..	..	*426*

Table A-18.—Average observed lengths and heights of warty-backs (**Quadrula nodulata**) of various ages from the 1966 Illinois River collections.[a]

Age in Years	*Average Length in Inches*	*Average Height in Inches*	*Number of Mussels*
5	1.7	1.4	3
6	1.8	1.4	5
7	1.9	1.5	8
8	2.0	1.7	7
9	2.1	1.7	18
10	2.2	1.8	9
11	2.2	1.8	6
12	2.3	1.8	6
13	2.4	1.9	2
14	2.2	1.8	1
Total	..	..	*65*

[a] Three specimens collected were not aged.

Table A-19.—Average observed lengths and heights of rock pocketbooks (**Arcidens confragosus**) of various ages from the 1966 Illinois River collections.

Age in Years	*Average Length in Inches*	*Average Height in Inches*	*Number of Mussels*
5	2.6	1.8	2
6	2.5	1.7	5
7	3.0	2.0	10
8	3.1	2.1	18
9	3.3	2.3	19
10	3.8	2.6	4
11	3.9	2.6	7
12	4.0	2.6	4
13	4.5	2.8	4
14	3.7	2.7	1
15	4.1	2.7	1
Total	..	..	*75*

Table A-20.—Average observed lengths and heights of three-horned warty-backs (**Obliquaria reflexa**) of various ages from the 1966 Illinois River collections.

Age in Years	*Average Length in Inches*	*Average Height in Inches*	*Number of Mussels*
4	1.8	1.2	2
5	1.2	0.9	1
6	1.7	1.2	5
7	1.7	1.3	13
8	1.6	1.2	7
9	1.9	1.4	10
10	2.0	1.5	4
11	1.8	1.4	4
12	..	..	0
13	2.1	1.6	2
14	..	..	0
15	2.1	1.6	1
Total	..	..	*49*

Table A-21.—Distribution of mussels in the mainstream of the Illinois River since 1870.

Kind of Mussel	*Upper River*[a]	*Peoria Pool*	*La Grange Pool*	*Alton Pool*
Cumberlandia monodonta	A[b]	A	P	P
Fusconaia ebena	P	P	P	P
Fusconaia flava f. *flava*	P	P	P	A
Fusconaia flava f. *undata*	P	P	P	P
Megalonaias gigantea	A	P	P	P
Amblema plicata	P	P	P	P
Quadrula quadrula	P	P	P	P
Quadrula pustulosa	P	P	P	P
Quadrula nodulata	P	P	P	P
Quadrula metanevra	P	P	P	P
Tritogonia verrucosa	P	P	P	P
Cyclonaias tuberculata	P	P	P	P
Plethobasus cyphyus	P	P	P	P
Pleurobema coccineum f. *solida*	P(?)	P	P	P
Pleurobema pyramidatum	P(?)	P(?)	P(?)	P(?)
Elliptio crassidens	P	P	P	P
Elliptio dilatatus	P	P	P	P
Arcidens confragosus	A	P	P	P
Lasmigona costata	P	A	P	A
Lasmigona complanata	P	P	P	P
Anodonta grandis grandis	P(?)	P	P	P(?)
Anodonta grandis corpulenta	P	P	P	P
Anodonta imbecillis	P	P	P	P
Anodonta suborbiculata	A	P	P	P
Alasmidonta calceolus	P	A	A	A
Alasmidonta marginata	P	P	A	A
Strophitus undulatus	A(?)	P	P	P
Anodontoides ferussacianus	A	P	A	A
Obliquaria reflexa	P	P	P	P
Obovaria olivaria	P	P	P	P
Actinonaias ligamentina	P	P	P	P
Plagiola lineolata	P	P	P	P
Truncilla truncata	P	P	P	P
Truncilla donaciformis	P	P	P	P
Leptodea fragilis	P	P	P	P
Proptera alata	A	P	P	P
Proptera capax	P	A	P	P
Proptera laevissima	A	P	P	P
Carunculina parva	A	P	P	P
Ligumia recta	P	P	P	P
Villosa iris iris	P	A	A	A
Lampsilis anodontoides f. *anodontoides*	P	P	P	P
Lampsilis anodontoides f. *fallaciosa*	P	P	P	P
Lampsilis radiata luteola	P	P	P	P
Lampsilis ventricosa	P	P	P	P
Lampsilis orbiculata f. *orbiculata*	A	A	A	P
Lampsilis orbiculata f. *higginsii*	P	P	P	P
Dysnomia triquetra	P	A	P	A
Total Recorded Kinds of Mussels Since 1870	*38*	*41*	*43*	*41*
Total Recorded Kinds of Mussels Taken Alive in 1966–1969	*0*	*16*	*18*	*20*

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[a] From the confluence of the Kankakee and Des Plaines rivers to Starved Rock dam.

[b] P designates present and A designates no record of the occurrence of the species.

Table A-22.—Kinds of mussels taken alive from the mainstream of the Illinois River in the vicinities of Henry and Chillicothe in 1912[a] and 1966.

Kind of Mussel	*Henry*		*Chillicothe*	
	1912	1966	1912	1966
F. ebena (Ebony Shell)	P[b]	A	P	A
F. f. f. *undata* (Pig-Toe)	P	A	P	A
M. gigantea (Washboard)	P	P	P	A
A. plicata (Three-Ridge)	P	P	P	P
Q. quadrula (Maple-Leaf)	P	A	P	A
Q. pustulosa (Pimple-Back)	P	A	P	A
T. verrucosa (Buckhorn)	P	A	P	A
C. tuberculata (Purple Warty-Back)	A	A	P	A
E. crassidens (Elephant's Ear)	A	A	P	A
E. dilatatus (Lady-Finger)	P	A	P	A
A. confragosus (Rock Pocketbook)	P	A	P	A
L. complanata (White Heel-Splitter)	P	A	P	A
A. g. grandis (Floater)	P	P	P	A
A. g. corpulenta (Floater)	P	P	P	A
A. imbecillis (Paper Pond Shell)	P	P	P	A
S. undulatus (Squaw Foot)	P	A	P	A
O. reflexa (Three-Horned Warty-Back)	A	A	P	A
A. ligamentina (Mucket)	P	A	P	A
P. lineolata (Butterfly)	P	A	P	A
T. truncata (Deer-Toe)	P	A	P	A
L. fragilis (Fragile Paper Shell)	P	P	P	A
P. alata (Pink Heel-Splitter)	P	P	P	A
P. laevissima (Fragile Heel-Splitter)	P	P	P	A
C. parva (Liliput Shell)	P	A	P	A
L. a. f. *anodontoides* (Yellow Sand-Shell)	P	A	P	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P	P	P
L. r. luteola (Fat Mucket)	P	A	P	A
L. o. f. *higginsii* (Higgin's Eye)	A	A	P	A

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[a] Forbes & Richardson (1913:533 & 536) and Danglade (1914:37).
[b] P designates present and A designates absent.

Table A-23.—Kinds of mussels taken alive from Peoria Lake in 1912, and in the 1924-1925 and 1966-1969 periods.

Kind of Mussel	*1912*[a]	*1924–1925*[a]	*1966–1969*
F. ebena (Ebony Shell)	P[b]	A	A
F. flava f. *flava* (Wabash Pig-Toe)	P	A	A
F. flava f. *undata* (Pig-Toe)	P	P	P
M. gigantea (Washboard)	P	A	P
A. plicata (Three-Ridge)	P	P	P
Q. quadrula (Maple-Leaf)	P	P	P
Q. pustulosa (Pimple-Back)	P	P	A[c]
Q. metanevra (Monkey-Face)	P	A	A
T. verrucosa (Buckhorn)	P	A	A[c]
C. tuberculata (Purple Warty-Back)	P	A	A
P. coccineum f. *solida*	P	A	A
E. dilatatus (Lady-Finger)	P	P	A
A. confragosus (Rock Pocketbook)	P	A	P
L. complanata (White Heel-Splitter)	P	P	P
A. g. grandis (Floater)	P	A	P
A. g. corpulenta (Floater)	P	P	P
A. imbecillis (Paper Pond Shell)	P	P	A
A. suborbiculata (Heel-Splitter)	P	P	A
S. undulatus (Squaw Foot)	P	A	A
O. reflexa (Three-Horned Warty-Back)	P	P	A
O. olivaria (Hickory-Nut)	P	A	A
A. ligamentina (Mucket)	P	A	A
P. lineolata (Butterfly)	P	A	A
T. truncata (Deer-Toe)	P	A	A
T. donaciformis (Fawn's Foot)	P	A	A
L. fragilis (Fragile Paper Shell)	P	P	P
P. alata (Pink Heel-Splitter)	P	P	A
P. laevissima (Fragile Heel-Splitter)	P	P	P
C. parva (Liliput Shell)	P	P	A
L. recta (Black Sand-Shell)	P	A	A
L. a. f. *anodontoides* (Yellow Sand-Shell)	P	A	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P	P
L. r. luteola (Fat Mucket)	P	P	P
L. ventricosa (Pocketbook)	P	A	A
L. o. f. *higginsii* (Higgin's Eye)	P	A	A

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[a] Danglade (1914:37) and Richardson (1928:457).
[b] P designates present and A designates absent.
[c] Taken alive in 1969 immediately below Peoria Lake.

Table A-24.—Kinds of mussels taken alive from the mainstream of the Illinois River between the Peoria lock and dam and Havana in 1912 and 1966 and from Quiver Lake in 1966.[a]

Kind of Mussel	*Mainstream*		*Quiver Lake*
	1912	1966	1966
F. ebena (Ebony Shell)	P[b]	A	A
F. f. f. *undata* (Pig-Toe)	P	P	A
M. gigantea (Washboard)	P	A	P
A. plicata (Three-Ridge)	P	P	P
Q. quadrula (Maple-Leaf)	P	P	P
Q. pustulosa (Pimple-Back)	P	A	P
Q. nodulata (Warty-Back)	P	A	A
T. verrucosa (Buckhorn)	P	A	A
C. tuberculata (Purple Warty-Back)	P	A	A
E. dilatatus (Lady-Finger)	P	A	A
A. confragosus (Rock Pocketbook)	P	P	A
L. complanata (White Heel-Splitter)	P	P	A
A. g. grandis (Floater)	P	A	P
A. g. corpulenta (Floater)	P	P	A
A. imbecillis (Paper Pond Shell)	P	P	A
A. suborbiculata (Heel-Splitter)	P	A	A
S. undulatus (Squaw Foot)	P	A	A
O. reflexa (Three-Horned Warty-Back)	P	A	P
A. ligamentina (Mucket)	P	A	A
P. lineolata (Butterfly)	P	A	A
T. truncata (Deer-Toe)	P	A	A
T. donaciformis (Fawn's Foot)	P	A	A
L. fragilis (Fragile Paper Shell)	P	P	A
P. alata (Pink Heel-Splitter)	P	P	A
P. capax (Fat Pocketbook)	P	A	A
P. laevissima (Fragile Heel-Splitter)	P	P	A
L. recta (Black Sand-Shell)	P	A	A
L. a. f. *anodontoides* (Yellow Sand-Shell)	P	A	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P	A
L. r. luteola (Fat Mucket)	P	A	P
L. ventricosa (Pocketbook)	P	A	A
L. o. f. *higginsii* (Higgin's Eye)	P	A	A

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[a] Danglade (1914:37) and 1966 survey.
[b] P designates present and A designates absent.

Table A-25.—Kinds of mussels taken alive from the mainstream of the Illinois River (including Bath Chute) from below Havana to the La Grange lock and dam in 1912 and 1966.[a]

Kind of Mussel	*1912*	*1966*
F. ebena (Ebony Shell)	P[b]	A
F. f. f. *undata* (Pig-Toe)	P	A
M. gigantea (Washboard)	P	P
A. plicata (Three-Ridge)	P	P
Q. quadrula (Maple-Leaf)	P	P
Q. pustulosa (Pimple-Back)	P	P
Q. nodulata (Warty-Back)	P	P
Q. metanevra (Monkey-Face)	P	A
T. verrucosa (Buckhorn)	P	A
C. tuberculata (Purple Warty-Back)	P	A
P. cyphyus (Bullhead)	P	A
P. coccineum f. *solida*	P	A
E. crassidens (Elephant's Ear)	P	A
E. dilatatus (Lady-Finger)	P	A
A. confragosus (Rock Pocketbook)	P	P
L. costata (Fluted Shell)	P	A
L. complanata (White Heel-Splitter)	P	P
A. g. grandis (Floater)	P	P
A. g. corpulenta (Floater)	P	P
A. imbecillis (Paper Pond Shell)	P	A
A. suborbiculata (Heel-Splitter)	P	A[c]
S. undulatus (Squaw Foot)	P	A
O. reflexa (Three-Horned Warty-Back)	P	A
A. ligamentina (Mucket)	P	A
P. lineolata (Butterfly)	P	A
T. truncata (Deer-Toe)	P	P
T. donaciformis (Fawn's Foot)	P	A
L. fragilis (Fragile Paper Shell)	P	P
P. alata (Pink Heel-Splitter)	P	A
P. capax (Fat Pocketbook)	P	A
P. laevissima (Fragile Heel-Splitter)	P	P
L. recta (Black Sand-Shell)	P	A
L. a. f. *anodontoides* (Yellow Sand-Shell)	P	A
L. a. f. *fallaciosa* (Slough Sand-Shell)	P	P
L. r. luteola (Fat Mucket)	P	P
L. ventricosa (Pocketbook)	P	A
L. o. f. *higginsii* (Higgin's Eye)	P	A

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[a] Danglade (1914:37) and 1966 survey.

[b] P designates present and A designates absent.

[c] A single specimen of this species was collected in 1966 at Lake Matanzas, a bottomland lake adjacent to the river below Havana.

Table A-26.—Locations of Illinois River mussel beds fished by commercial mussel fishermen in 1966.[a]

River Mile	*River Bank*	*River Mile*	*River Bank*
0.3– 2.0	Left	48.0–48.9	Right
5.0– 5.5	Right	50.7–51.5	Right
10.3–10.5	Right	53.0–53.9	Left
13.2–13.5	Right	54.0–54.7	Right
14.5–14.7	Left	55.9–56.4	Left
14.9–15.1	Right	57.8–59.1	Right
19.0–19.5	Right	60.4–61.5	Right
23.2–23.5	Right	62.1–62.6	Right
24.2–24.4	Left	63.8–64.5	Right
27.7–27.9	Left	65.9–66.5	Left
28.1–29.5	Right	66.6–66.9	Right
30.5–31.3	Right	68.9–69.4	Right
33.0–33.5	Right	72.6–74.3	Right
37.3–37.6	Right	74.5–75.1	Left
39.1–39.3	Right	75.2–75.8	Right
40.1–40.8	Right	79.0–79.9	Right
41.2–42.4	Left	80.4–80.8	Right
44.0–44.9	Right	83.5–83.7	Right
45.2–45.4	Left	86.4–87.0	Left
46.8–47.7	Left		

[a] Based on observations of mussel fishing by the Illinois Natural History Survey crew and on interviews with commercial mussel fishermen. In 1969 commercial mussel fishing was conducted on beds located immediately below Peoria Lake and in Middle and Lower Peoria lakes, as discussed in the text.

Table A-27.—Estimates of standing crops of mussels in some of the beds fished commercially and in two unfished beds in the Illinois River in 1966.

River Mile	*River Bank*	*Live Weights[a] of All Species in Pounds Per Acre*	*Shell Weights[b] of Commercial Species in Pounds Per Acre*	
			All Sizes	Height 2.5 Inches or More
1.0	Left	1,480	939	493
5.5	Right	625	282	119
10.5	Right	246	130	51
15.0	Right	462	294	138
19.4	Right	767	512	297
29.0	Right	1,375	816	493
30.6	Right	885	541	374
42.3	Left	845	561	164
48.3	Right	669	444	227
51.2	Right	3,233	2,092	1,312
53.6	Left	476	324	183
54.3	Right	643	267	88
60.8	Right	672	427	288
66.9	Right	756	525	179
72.9	Right	2,443	1,591	651
86.8	Left	648	337	312
162.3[c]	Left	6,040	3,762	2,030
168.2[c]	Right	1,457	949	536

[a] Live mussels, including shells and bodies.
[b] Includes only the weights of the shells of mussels taken alive.
[c] Not fished commercially in 1966, but was fished in 1969.

Table A-28.—Number of mussels caught per 5 minutes of fishing with the exploratory crowfoot bar in the 1966 survey of the Illinois River.

Kind of Mussel	*Mussels Caught Per 5 Minutes of Fishing*				
	Alton Pool	La Grange Pool	Peoria Pool	Alton, La Grange, and Peoria Pools	Entire River[a]
Fusconaia ebena	*[b]	0.0	0.0	*	*
Fusconaia f. f. *undata*	0.1	*	*	*	*
Megalonaias gigantea	0.6	0.1	0.0	0.2	0.2
Amblema plicata	4.8	0.7	0.6	1.7	1.6
Quadrula quadrula	0.8	0.3	0.1	0.3	0.3
Quadrula pustulosa	1.4	*	0.0	0.4	0.4
Quadrula nodulata	0.1	*	0.0	*	*
Arcidens confragosus	0.2	*	*	0.1	0.1
Lasmigona complanata	*	*	*	*	*
Anodonta g. grandis	0.0	*	*	*	*
Anodonta g. corpulenta	0.1	*	*	0.1	*
Anodonta imbecillis	0.0	0.0	0.0	0.0	0.0
Anodonta suborbiculata	0.0	0.0	0.0	0.0	0.0
Obliquaria reflexa	0.1	0.0	0.0	*	*
Obovaria olivaria	*	0.0	0.0	*	*
Truncilla truncata	*	*	0.0	*	*
Truncilla donaciformis	0.0	0.0	0.0	0.0	0.0
Leptodea fragilis	0.1	0.1	*	0.1	*
Proptera alata	*	*	*	*	*
Proptera laevissima	*	*	*	*	*
Carunculina parva	0.0	0.0	0.0	0.0	0.0
Lampsilis a. f. *fallaciosa*	*	*	*	*	*
Lampsilis r. luteola	0.0	*	*	*	*
Total	*8.3*	*1.2*	*0.7*	*2.9*	*2.6*

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[a] Includes Starved Rock and Marseilles navigation pools. No live mussel was taken in these pools in the 1966 survey.

[b] Denotes less than 0.1 mussel caught per 5 minutes of fishing.

Table A-29.—Number of mussels caught per 5 minutes of fishing with the dredge in the 1966 survey of the Illinois River.

Kind of Mussel	*Mussels Caught Per 5 Minutes of Fishing*			
	Alton Pool	La Grange Pool	Peoria Pool	Alton, La Grange, and Peoria Pools[a]
Fusconaia ebena	0.0	0.0	0.0	0.0
Fusconaia f. f. *undata*	0.2	0.0	0.2	0.1
Megalonaias gigantea	2.8	0.3	0.0	0.6
Amblema plicata	26.1	3.0	5.1	8.5
Quadrula quadrula	6.1	0.9	0.6	1.7
Quadrula pustulosa	5.8	0.1	0.0	1.1
Quadrula nodulata	0.7	0.1	0.0	0.2
Arcidens confragosus	1.0	0.2	0.0	0.3
Lasmigona complanata	0.0	0.1	*[b]	*
Anodonta g. grandis	0.0	0.0	0.0	0.0
Anodonta g. corpulenta	0.4	0.2	0.2	0.2
Anodonta imbecillis	0.1	0.0	*	*
Anodonta suborbiculata	0.0	0.0	0.0	0.0
Obliquaria reflexa	1.7	0.0	0.0	0.3
Obovaria olivaria	0.0	0.0	0.0	0.0
Truncilla truncata	0.4	0.0	0.0	0.1
Truncilla donaciformis	0.0	0.0	0.0	0.0
Leptodea fragilis	0.5	0.1	*	0.1
Proptera alata	0.0	0.0	0.0	0.0
Proptera laevissima	0.0	0.0	0.0	0.0
Carunculina parva	0.0	0.0	0.0	0.0
Lampsilis a. f. *fallaciosa*	0.1	0.0	0.1	*
Lampsilis r. luteola	0.0	0.0	0.0	0.0
Total	*45.9*	*5.0*	*6.2*	*13.2*

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[a] The dredge was not used in the Starved Rock and Marseilles navigation pools.
[b] Denotes less than 0.1 mussel caught per 5 minutes of fishing.

Table A-30.—Number of mussels caught per man-hour of fishing by wading in the 1966 survey of the Illinois River.

Kind of Mussel	*Mussels Caught Per Man-Hour of Fishing*				
	Alton Pool	La Grange Pool	Peoria Pool	Alton, La Grange, and Peoria Pools	Entire River[a]
Fusconaia ebena	0.0	0.0	0.0	0.0	0.0
Fusconaia f. f. *undata*	1.2	0.0	0.3	0.4	0.4
Megalonaias gigantea	1.7	0.3	*[b]	0.6	0.6
Amblema plicata	25.8	10.3	14.1	16.1	15.5
Quadrula quadrula	3.3	0.7	0.0	1.1	1.0
Quadrula pustulosa	4.9	0.2	0.0	1.3	1.3
Quadrula nodulata	2.2	0.1	0.0	0.6	0.6
Arcidens confragosus	0.1	0.5	0.0	0.2	0.2
Lasmigona complanata	0.0	0.1	0.0	*	*
Anodonta g. grandis	0.0	0.1	0.1	*	*
Anodonta g. corpulenta	1.6	1.1	1.6	1.4	1.4
Anodonta imbecillis	0.1	0.2	0.0	0.1	0.1
Anodonta suborbiculata	0.0	0.1	0.0	*	*
Obliquaria reflexa	0.5	0.1	0.0	0.2	0.1
Obovaria olivaria	0.0	0.0	0.0	0.0	0.0
Truncilla truncata	0.2	0.1	0.0	0.1	0.1
Truncilla donaciformis	0.1	0.0	0.0	*	*
Leptodea fragilis	1.1	0.3	*	0.4	0.4
Proptera alata	0.5	0.0	0.1	0.2	0.2
Proptera laevissima	1.6	0.7	0.2	0.7	0.7
Carunculina parva	0.1	0.0	0.0	*	*
Lampsilis a. f. *fallaciosa*	1.9	0.3	0.4	0.8	0.7
Lampsilis r. luteola	0.0	0.1	0.2	0.1	0.1
Total	*46.9*	*15.3*	*17.0*	*24.3*	*23.4*

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[a] Includes Starved Rock and Marseilles navigation pools. No live mussel was taken in these pools in the 1966 survey.

[b] Denotes less than 0.1 mussel caught per man-hour of fishing.

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BULLETIN

Volume 29, Article 2.—Stocking and Sport Fishing at Lake Glendale (Illinois). By Donald F. Hansen. July, 1966. 54 p., frontis., 9 fig., bibliogr., index.

Volume 29, Article 3.—Hybridization of Four Species of Sunfishes (Centrarchidae). By William F. Childers. September, 1967. 55 p., frontis., 2 fig., color plate, bibliogr., index.

Volume 29, Article 4.—The Thrips, or Thysanoptera, of Illinois. By Lewis J. Stannard. May, 1968. 338 p., frontis., 310 fig., bibliogr., index.

Volume 30, Article 1.—Largemouth Bass and Other Fishes in Ridge Lake, Illinois, 1941-1963. By George W. Bennett, H. Wickliffe Adkins, and William F. Childers. September, 1969. 67 p., 10 fig., bibliogr., index.

Volume 30, Article 2.—Dynamics of One-Species Populations of Fishes in Ponds Subjected to Cropping and Additional Stocking. By D. Homer Buck and Charles F. Thoits III. March, 1970. 97 p., 10 fig., bibliogr., index.

Volume 30, Article 3.—Migrational Behavior of Mallards and Black Ducks as Determined from Banding. By Frank C. Bellrose and Robert D. Crompton. September, 1970. 68 p., frontis., 25 fig., bibliogr., index.

Volume 30, Article 4.—Fertilization of Established Trees: A Report of Field Studies. By Dan Neely, E. B. Himelick, and Webster R. Crowley, Jr. September, 1970. 32 p., frontis., 8 fig., bibliogr., index.

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Natural History Survey

BULLETIN

Comparative Uptake and Biodegradability of DDT and Methoxychlor by Aquatic Organisms

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der P. Kapoor
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Frontispiece. — Organisms and compounds used in this investigation. On a background of daphnia swimming in wat
re (top to bottom) the green sunfish, guppy, tilapia, and snails.

Comparative Uptake and Biodegradability of DDT and Methoxychlor by Aquatic Organisms

Keturah A. Reinbold
Inder P. Kapoor
William F. Childers
Willis N. Bruce
Robert L. Metcalf

DDT IS SOLUBLE in water to about 0.002 ppm, but it is soluble in animal fats to about 100,000 ppm. Because DDT possesses such a high lipid-to-water partition value and resists attack by multifunction oxidase detoxifying enzymes, this insecticide has become a ubiquitous environmental pollutant and is found in animal tissues everywhere. For example, DDT is present in Lake Michigan bottom muds at about 0.014 ppm. It has been found in concentrations of 3–6 ppm in fishes, such as coho salmon and lake trout, taken from Lake Michigan and in even higher concentrations in the tissues of fish-eating birds living near the lake (Harrison et al. 1970:505). DDT used for spruce budworm control in the Yellowstone River system was found to persist in the aquatic environment for more than 2 years (Cope 1961:242-244). Bridges et al. (1963) found concentrations of DDT in a number of organisms in a farm pond treated with 0.02 ppm of DDT. Fish in aquaria have been shown to eliminate DDT very slowly after a single sublethal exposure (Gakstatter & Weiss 1967:305). Because animals concentrate DDT in their tissues and eliminate it very slowly, aquatic pollution by DDT, whether it results directly from blackfly and mosquito control programs or indirectly from urban treatments for elm bark beetle control or agricultural applications for fruit pests, is particularly deleterious to environmental quality.

The need for a persistent but biodegradable substitute for DDT is urgent. Methoxychlor is being widely considered as such a substitute, especially for control of blackflies, bark beetles, and fruit and garden pests. It has been reported that, after 28 days of exposure to 0.04 ppm of methoxychlor, bluegills had metabolized or excreted most of the compound which they had taken up. After 56 days no methoxychlor was found in the fish (Kennedy et al. 1970:12). Preliminary studies in a laboratory model ecosystem (Kapoor et al. 1970:1151) indicate that methoxychlor does not accumulate in fishes, as does DDT, but reaches a dynamic equilibrium.

The studies reported in this paper were designed to further test the biodegradability of methoxychlor and to compare in a laboratory aquatic environment (i) the uptake of DDT and methoxychlor directly from water by fishes, from water by crustaceans of the genus *Daphnia* and by snails of the genus *Physa*, and from daphnia by guppies in a daphnia-to-fish food chain and (ii) the subsequent elimination of the insecticides from the organisms.

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We are indebted to several members of the Illinois Natural History Survey staff for their contributions to this investigation. Dr. William H. Luckmann, Head of the Section of Economic Entomology, provided encouragement throughout the study and reviewed the manuscript, which was edited by Robert M. Zewadski, Associate Technical Editor. Richard M. Sheets, Technical Illustrator, prepared the graphs and designed the frontispiece, and Wilmer D. Zehr, Technical Photographer, provided most of the photographs. The photograph of the tilapia appearing in the frontispiece was loaned by the Section of Aquatic Biology.

We wish to thank the Natural History Survey and the University of Illinois for the laboratory space and equipment provided for this investigation.

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MATERIALS AND METHODS

Radiolabeled Compounds

The investigations were conducted with ^{3}H-ring substituted methoxychlor obtained by the procedure of Kapoor et al. (1970:1146). The compound was 99.9+ percent pure according to our evaluation of it by thin-layer chromatography, and it had a specific activity of 4.81 mC/mM. Ring-labeled ^{14}C-DDT was obtained from the World Health Organization of the United Nations, Geneva, Switzerland. The DDT had a specific activity of 5.48 mC/mM and a purity of 99.9+ percent.

Radioassay Methods

The radioactivity in 1-ml water samples containing radiolabeled compounds was counted in 10 ml of ^{3}H scintillation fluid (200 grams of naphthalene, 10 grams of PPO, 0.25 gram of POPOP in dioxane to make 1 liter) in a Beckman S-250 scintillation counter. All organisms used in our investigations were freeze-dried and ground to a powder with a mortar and pestle. Each of three 10-mg portions of each sample of the powdered material was placed in 15 ml of scintillation fluid. The samples were kept in the dark overnight before counting to quench phosphorescence. The radioactivity in each sample was determined by averaging the results of the three counts. Quenching, if any occurred, was corrected for, using the appropriate quench curves. All insecticide concentrations in the organisms were calculated on a dry-weight basis.

Chromatographic Techniques

Thin-layer chromatography (TLC) was performed in the usual manner using glass plates coated with 0.25 mm of silica gel. To determine the relative proportions of parent compounds and their metabolites in tilapia (*Tilapia mossambica*) and green sunfish (*Lepomis cyanellus*), portions of the powdered organisms were extracted with acetonitrile (2 ml for tilapia, 4 ml for green sunfish). About 0.05 ml of the extract from each sample was spotted on a TLC plate. Non-radiolabeled parent compounds and model metabolites were incorporated as internal standards for cochromatography by spotting them on the plate over the acetonitrile extracts of the fishes. Methoxychlor chromatograms were developed in a solvent system consisting of 3 parts diethyl ether and 1 part petroleum ether (b. p. 60° to 68° C), and those of DDT in petroleum ether (b. p. 60° to 68° C) alone.

Radioautographs of the ^{14}C-labeled DDT metabolites were made by exposing Eastman Kodak No Screen Medical X-ray film to the developed chromatograms. Black spots which had developed on the film were matched with the incorporated internal standards to determine the identity of the metabolites. The corresponding areas of silica gel were scraped from the chromatograms and counted by scintillation counting; from these counts the relative percentages of each parent compound and its metabolites were then calculated. The relative proportions of methoxychlor and its metabolites were determined by scraping appropriate spots or strips of silica gel from the chromatograms and radioassaying them.

Bioassay Methods

We used cylindrical Pyrex jars 8 inches deep and 8¼ inches in diameter in all of the experiments reported on here. Each jar contained 5 liters of synthetic hard water (Cairns 1969:8) and was covered by a plate glass lid. The water was constantly aerated by compressed air bubbling through a glass tube extending down the inside wall of the jar. Both DDT and methoxychlor were added to the water in these jars from standard 0.0025-percent solutions in acetone. The water-insecticide solutions were allowed to equilibrate for 24 hours before any aquatic organisms were placed in the jars.

The animals used were daphnia (*Daphnia magna*) (hereafter referred to as "daphnia"), snails (*Physa* sp.) (hereafter referred to as "snails"), tilapia (*Tilapia mossambica*) (hereafter referred to as "tilapia"), green sunfish (*Lepomis cyanellus*), and guppies (*Lebistes reticulatus*). At 2-day, 3-day, or 10-day intervals, the organisms were moved to fresh water or were surface rinsed with clean water and then frozen. Subsequently, the organisms were freeze-dried, powdered, and radioassayed. In all experiments organisms held under the same conditions as were the test animals but not exposed to insecticides were prepared and assayed in the same manner as were the test samples.

Comparative uptake of DDT and methoxychlor from water by two fish species, tilapia and green sunfish, was studied at insecticide levels of 0.001, 0.003, and 0.01 ppm. The tilapia experiment was duplicated using three fish (0.6–1.8 grams per fish) in each jar. Two jars of tilapia were used at each of the three levels of each insecticide (12 jars). Only one green sunfish (5–9 grams) was placed in each of three jars at each concentration of each compound (18 jars). One fish was removed from each jar (two tilapia from each insecticide concentration and one green sunfish from each concentration) on the 3rd, 10th, and 31st days, after which the experiment was terminated. On the 10th and 20th days those fishes which remained were transferred to jars containing insecticide concentrations equivalent to those in which the fishes had been placed at the beginning of the experiment.

The uptake of insecticides from water by daphnia (1 gram per jar) was studied at the insecticide levels used in the fish experiments. The daphnia from half of the jars at each concentration of each insecticide were removed on the 3rd day and from the remaining jars on the 6th day. All samples were then radioassayed.

In another experiment tilapia weighing 0.2–1.4 grams each were exposed, five fish per jar in each of five jars for each insecticide, to 0.003 ppm of DDT or methoxychlor for 12 days. At 3-day intervals one fish from each jar was removed for radioassay, and the rest were transferred to water freshly treated with 0.003 ppm of insecticide. After 12 days the remaining fish were moved to water containing no insecticide. Samples of one fish each were then taken after additional periods of 2, 5, 9, 11, 12, and 15 days and assayed for radioactivity to determine the comparative insecticide excretion rates.

Daphnia (2 grams) and snails (1 gram) were exposed together in jars to a level of 0.003 ppm of DDT or methoxychlor for 2, 4, or 6 days. In one series of jars the daphnia and snails were exposed for 2 days, the animals in one jar were removed for radioassay, and the remaining organisms were moved to water without insecticide. They were transferred to fresh water without insecticide every 2 days, and a one-jar sample was removed after 1, 2, 4, or 6 days. The organisms in another series of jars were transferred to water containing the original level of insecticide after 2 and 4 days. They were also sampled for radioassay after 4 days. After 6 days a sample was removed for radioassay, and the remaining organisms were moved to water without insecticide. Again, they were transferred to fresh water every 2 days and were sampled after 1, 3, or 5 days.

Insecticide uptake in a daphnia-to-guppy food chain was studied by holding 2–5 grams of daphnia in water containing 0.003 ppm of DDT or methoxychlor for 48 hours and then feeding them to guppies held in water without any insecticide. Three jars of daphnia exposed to methoxychlor were combined. One-third of these daphnia were analyzed for insecticide content by scintillation counting and the remaining animals were fed to guppies held in two jars, each containing 10 fish. The same procedure was followed with daphnia exposed to DDT and fed to two additional jars of fish. By exposing additional jars of daphnia to the insecticides at 2-day intervals, we repeated the process and fed the fish every other day. Fish were removed from each jar on the 6th, 8th, and 20th days and assayed for radioactivity.

RESULTS AND DISCUSSION

Uptake and Metabolism by Fishes

The results of the investigation of the uptake from water of DDT and methoxychlor by tilapia and green sunfish are presented in Table 1. At the 0.001-ppm level the concentration of methoxychlor in tilapia dropped from 0.8 ppm after 3 days of exposure to 0.2 ppm after 10 days, remaining at 0.2 ppm at the end of 31 days. The DDT concentration decreased from 1.3 ppm after 3 days to 0.7 after 10 days; it then increased markedly to 6.8 ppm at 31 days. The same pattern occurred at the higher insecticide levels. The pattern was repeated in the green sunfish, which differed from the tilapia, however, in having lower DDT-to-methoxychlor ratios. These lower ratios may have been the result of the green sunfish's lower proportion of body fat and its consequent smaller capacity for concentrating DDT in fat tissues.

The results show far greater contrasts when we examine the concentration factor (Fig. 1 and 2). While

Table 1. — Comparative uptake from water of ^{14}C-DDT and ^{3}H-methoxychlor by tilapia and green sunfish.

Insecticide Concentration in Water in ppm	*Days of Exposure to Insecticide*	*Insecticide Concentration[a] in ppm in Tilapia*		*Ratio of DDT to Methoxychlor*	*Insecticide Concentration[a] in ppm in Green Sunfish*		*Ratio of DDT to Methoxychlor*
		Methoxychlor	DDT		Methoxychlor	DDT	
0.001	3	0.8	1.3	1.6	0.8	0.5	0.6
	10	0.2	0.7	3.5	0.3	0.6	2.0
	31	0.2	6.8	34.0	0.2	3.9	19.5
0.003	3	1.8	4.4	2.4	• •	2.2	• • •
	10	0.3	2.5	8.3	0.6	1.7	2.8
	31	0.6	12.0	20.0	0.6	10.2	17.0
0.01	3	9.0	16.4	1.8	7.4	• • •	• • •
	10	1.0	13.9	13.9	1.9	8.6	4.5
	31	2.0	106.0	53.0	2.7	40.2	14.9

[a] All such concentrations were calculated on a dry-weight basis.

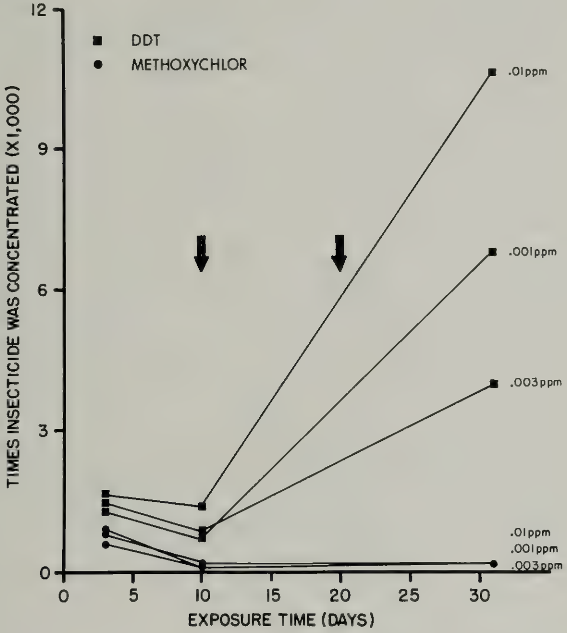

Fig. 1. — Comparative uptake from water of ^{14}C-DDT and ^{3}H-methoxychlor by tilapia. The vertical arrows indicate the days when fish were transferred to jars containing insecticide levels equivalent to those which the fish had been placed in at the beginning of the experiment.

the insecticide concentration in methoxychlor-exposed fishes reached an equilibrium, which indicated that the compound was being metabolized and excreted, DDT was increasingly concentrated in the fishes. In tilapia exposed to the 0.01-ppm insecticide level at the end of 31 days, even after the DDT had been concentrated 10,600 times it had not reached a steady state. Furthermore, when tilapia were held in water containing 0.003 ppm of insecticide for 12 days and subsequently were left for 15 days in jars containing water with no insecticide, the radioactive compounds in methoxychlor-exposed fish were rapidly excreted (Fig. 4). At the end of 15 days in uncontaminated water there was a 10,000-fold difference between the concentrations in tilapia of methoxychlor and of DDT (Table 4).

The metabolic pattern (Table 2) indicates that both fishes metabolized methoxychlor to a greater extent than they did DDT. Tilapia metabolized DDT to a greater extent than green sunfish metabolized it. Tilapia contained DDD as a major metabolite, but the major metabolite of the green sunfish was DDE. Methoxychlor was rapidly metabolized by tilapia, which contained considerably higher proportions of the mono-*O*-demethylated product [2-(*p*-methoxyphenyl)-2-(*p*-hydroxyphenyl)-1, 1, 1-trichloroethane] but only slightly greater proportions of the bis-*O*-demethylated metabolite [2, 2-bis-(*p*-hydroxyphenyl)-1, 1, 1-trichloroethane] than did the green sunfish.

The data from these experiments in-

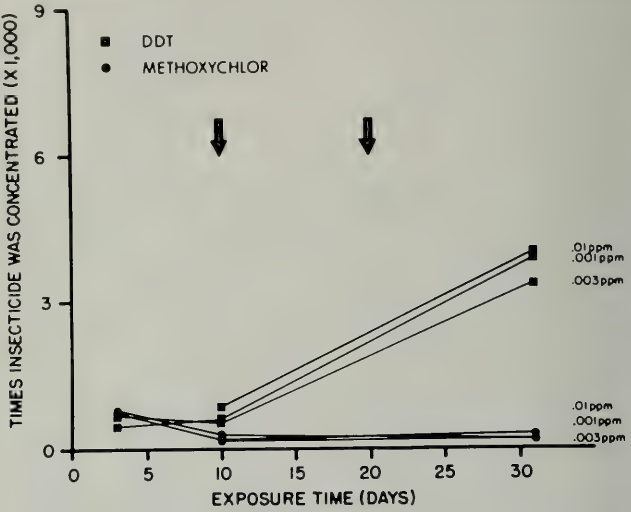

Fig. 2. — Comparative uptake from water of ^{14}C-DDT and ^{3}H-methoxychlor by green sunfish. The vertical arrows indicate the days when fish were transferred to jars containing insecticide levels equivalent to those which the fish had been placed in at the beginning of the experiment.

Table 2. — Distribution of ^{14}C-DDT and ^{3}H-methoxychlor and their metabolites in tilapia and green sunfish following exposure to water containing these insecticides.

Insecticide	*Insecticide Concentration in Water in ppm*	*Days of Exposure to Insecticide*	*Relative Percentages of Insecticides and Their Metabolites Found in Fishes*					
			In Tilapia			In Green Sunfish		
DDT			DDT	DDD	DDE	DDT	DDD	DDE
	0.001	3	62.5	37.5	0.0	100.0	0.0	0.0
		10	62.0	38.0	0.0	100.0	0.0	0.0
		31	66.0	29.0	5.0	91.0	1.0	8.0
	0.003	3	77.0	23.0	0.0	100.0	0.0	0.0
		10	56.0	37.0	7.0	100.0	0.0	0.0
		31	47.0	44.0	9.0	75.0	4.0	21.0
	0.01	3	76.0	24.0	0.0	• • •	• • •	• • •
		10	60.0	36.5	3.5	92.5	2.5	5.0
		31	76.0	20.0	4.0	90.0	3.0	7.0
Methoxychlor			A[a]	B[b]	C[b]	A[a]	B[b]	C[b]
	0.01	3	43.4	45.2	11.4	59.0	29.8	11.2
		31	13.9	71.3	14.8	66.3	26.9	6.8

[a] Parent material: $CH_3OC_6H_4HCCCl_3C_6H_4OCH_3$
[b] Metabolite B: $HOC_6H_4HCCCl_3C_6H_4OCH_3$
Metabolite C: $HOC_6H_4HCCCl_3C_6H_4OH$

dicate that methoxychlor is readily biodegradable in tilapia and green sunfish. It seems likely that this insecticide is also biodegradable in other fish species.

Uptake and Metabolism by Daphnia and Snails

Daphnia also concentrated both methoxychlor and DDT taken up from water. The DDT-to-methoxychlor ratio (Table 3) in daphnia after 3 days of exposure at the three insecticide levels used in these experiments ranged from 1.8 to 2.5, a pattern similar to that displayed by the fishes we studied.

When daphnia and snails were held together in jars containing 0.003 ppm of insecticide, daphnia concentrated the two insecticides at about the same rate, but the snails concentrated me-

Table 3. — Comparative uptake from water of ^{14}C-DDT and ^{3}H-methoxychlor by daphnia.

Insecticide Concentration in Water in ppm	*Days of Exposure to Insecticide*	*Insecticide Concentration[a] in ppm in Daphnia*		*Ratio of DDT to Methoxychlor*
		Methoxychlor	DDT	
0.001	3	11	28	2.5
	6	9	15	1.7
0.003	3	37	66	1.8
	6	22	32	1.5
0.01	3	143	316	2.2
	6	• • •	83	• •

[a]All such concentrations were calculated on a dry-weight basis.

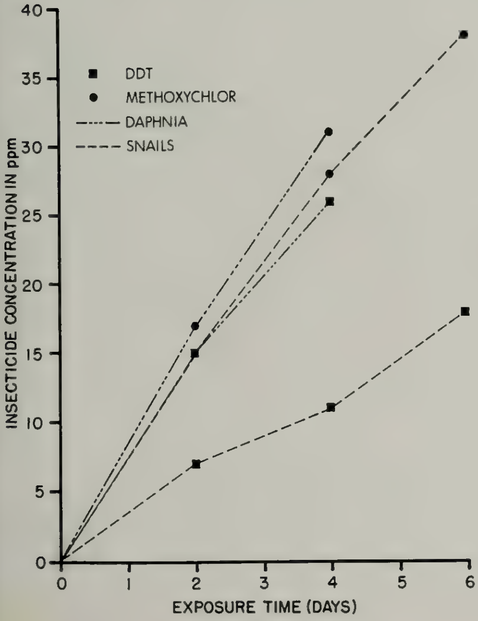

Fig. 3. — Comparative uptake of ^{14}C-DDT and ^{3}H-methoxychlor by snails and daphnia following exposure to a 0.003-ppm insecticide level in water.

Table 4. — Comparative uptake and excretion of ^{14}C-DDT and ^{3}H-methoxychlor by tilapia, daphnia, and snails on exposure to water containing 0.003 ppm of insecticide and subsequently to water with no insecticide.

Days of Exposure to Insecticide	*Days in Clean Water Following Exposure*	*Insecticide Concentration*[a] *in ppm in Tilapia*		*Ratio of DDT to Methoxychlor*	*Insecticide Concentration*[a] *in ppm in Daphnia*		*Ratio of DDT to Methoxychlor*	*Insecticide Concentration*[a] *in ppm in Snails*		*Ratio of DDT to Methoxychlor*
		Methoxychlor	DDT		Methoxychlor	DDT		Methoxychlor	DDT	
2	0	...	...	...	17.0	15.0	0.9	15.0	7.0	0.5
	1	...	...	...	11.0	10.0	0.9	14.0	5.0	0.4
	2	...	...	...	8.0	8.0	1.0	12.0	3.0	0.3
	4	...	...	...	2.0	5.0	2.5	12.0	3.0	0.3
	6	...	...	...	...	...	..	11.0	4.0	0.4
3	0	2.0	5.0	2.5	...	...	..	...	...	..
4	0	...	...	...	31.0	26.0	0.8	28.0	11.0	0.4
6	0	4.0	8.0	2.0	...	...	..	38.0	18.0	0.5
	1	...	...	...	...	...	..	...	13.0	..
	3	...	...	...	...	...	..	36.0	...	..
	5	...	...	...	...	...	..	23.0	10.0	0.4
9	0	5.0	11.0	2.2	...	...	..	...	...	..
12	0	8.0	13.0	1.6	...	...	..	...	...	..
	2	2.0	13.0	6.5	...	...	..	...	...	..
	5	2.0	...	...	...	...	..	...	...	..
	9	2.0	6.0	3.0	...	...	..	...	...	..
	11	...	4.0	...	...	...	..	...	...	..
	12	0.2	...	...	...	...	..	...	...	..
	15	0.0001	1.0	10,000.0	...	...	..	...	...	..

[a] All such concentrations were calculated on a dry-weight basis.

thoxychlor much more than they concentrated DDT—18 ppm of DDT:38 ppm of methoxychlor after 6 days of exposure to the insecticides (Table 4 and Fig. 3). When daphnia and snails were held in water free of insecticide after exposure to DDT or methoxychlor, both organisms excreted radioactive compounds. Daphnia excreted methoxychlor more rapidly than DDT, while the opposite was true of the snails (Table 4 and Fig. 4). The snails apparently cannot readily metabolize methoxychlor and, as a result, retain relatively persistent, high concentrations of that insecticide once they have taken it up. This observation agrees with that of Kapoor et al. (1970:1151). The snails, like the other organisms studied, also tend to retain DDT.

Uptake and Metabolism by Guppies in a Daphnia-to-Fish Food Chain

The results of the daphnia-to-guppy food chain study are shown in Table 5

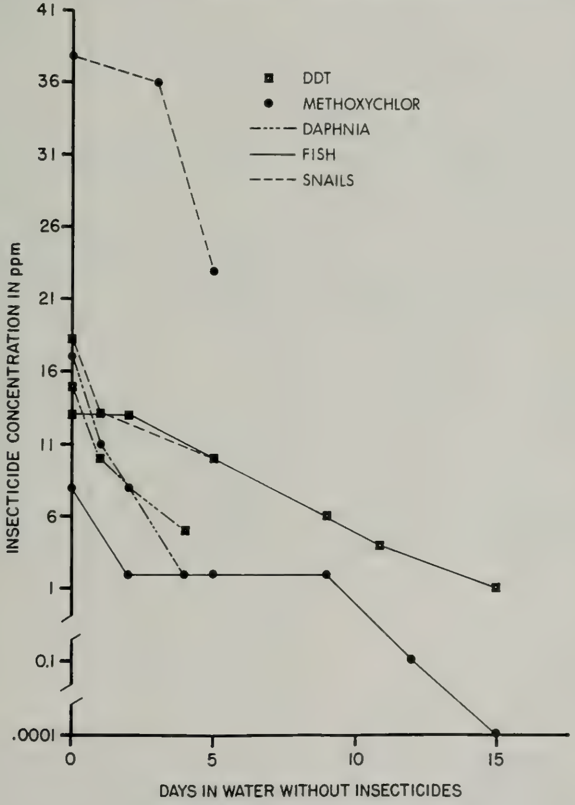

Fig. 4. — Loss of radioactivity from tilapia, snails, and daphnia in water without insecticides following exposure to 0.003 ppm of DDT or methoxychlor in water. Periods of exposure to insecticides: fish, 12 days; snails, 6 days; daphnia, 2 days.

Table 5. — Uptake of ^{14}C-DDT and ^{3}H-methoxychlor in a daphnia-to-guppy food chain.

Insecticide Concentration[a] *in Daphnia in ppm*	*Days Fish Fed on Daphnia Exposed to Insecticide*	*Insecticide Concentration*[a] *in Fish in ppm*	*Rate of Insecticide Uptake From Food By Fish* $\left(\frac{\text{ppm in Fish}}{\text{ppm in Daphnia}}\right)$	*Ratio of Rates of Uptake by Fish, DDT to Methoxychlor*
Methoxychlor				
22.6	6	0.14	0.006	• • •
21.3	8	0.07	0.003	• • •
21.7	20	0.17	0.008	• • •
DDT				
25.1	6	3.10	0.124	21.0
25.9	8	3.69	0.143	48.0
26.6	20	7.80	0.293	38.0

[a] All such concentrations were calculated on a dry-weight basis.

and Fig. 5. There was little difference in the uptake of the two insecticides from water by the daphnia. However, when the daphnia entered the food chain, the methoxychlor content in the fish rapidly reached a steady state, while the concentration of DDT continued to increase. From the 6th to the 20th day the methoxychlor level in the guppies increased only from 0.14 to 0.17 ppm, but the DDT level increased from 3.10 to 7.80 ppm. The differences in concentration of the two compounds are shown by the relative values of the rates of uptake by the fish from the daphnia (column 4 of Table 5) and by the ratios of the rates of uptake (column 5). The difference in accumulation is due to the presence of alkoxy groups on the aryl rings in methoxychlor, which cause it, unlike DDT, to be subject to attack by multifunction oxidases of the fish and, therefore, to be rapidly metabolized and excreted.

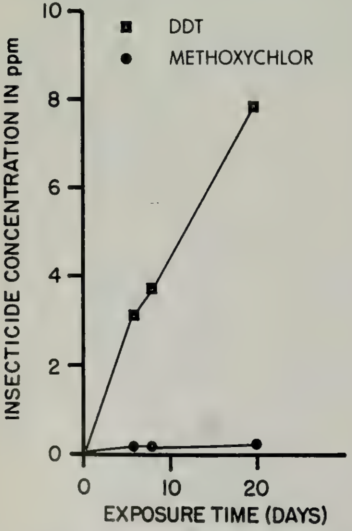

Fig. 5. — Uptake of ^{14}C-DDT and ^{3}H-methoxychlor by guppies in a daphnia-to-guppy food chain. The daphnia were held in water containing 0.003 ppm of DDT or methoxychlor for 48 hours before being fed to the fish.

In general, our investigations show that methoxychlor appears to be readily biodegradable in fishes and in some, though not all, other aquatic organisms. Thus, it seems to be a safer insecticide than DDT to use in or near aquatic environments.

SUMMARY

Comparative studies were made of the uptake and metabolism by three species of fishes, by daphnia, and by a snail of radiolabeled methoxychlor and DDT. Tilapia and green sunfish exposed over a 31-day period to the

radiolabeled insecticides at levels of 0.001, 0.003, and 0.01 ppm in water concentrated DDT as much as 10,600-fold and methoxychlor about 200-fold. However, when tilapia were transferred to water with no insecticide following 12 days of exposure to 0.003 ppm of insecticide in water, the residues of methoxychlor decreased within 15 days from 8 ppm to 0.0001 ppm and DDT from 13 to 1 ppm, a 10,000-fold difference between the concentrations of DDT and methoxychlor.

Significant differences were found between the rates at which tilapia and green sunfish metabolized DDT and methoxychlor. Tilapia metabolized DDT to a greater extent and contained DDD as a major metabolite, while green sunfish contained only small amounts of DDD. Tilapia also metabolized methoxychlor more rapidly than green sunfish metabolized it and contained higher amounts of mono- and bis-phenols produced by *O*-demethylation.

Daphnia in water containing DDT or methoxychlor concentrated DDT at nearly the same rate at which they concentrated methoxychlor to about twice that rate. When daphnia containing either radiolabeled DDT or methoxychlor were fed to guppies to complete a food chain, DDT was rapidly concentrated in the fish, reaching levels of about 8 ppm in 20 days, while methoxychlor concentrations never rose beyond 0.17 ppm. Thus, methoxychlor appears readily biodegradable in fishes. However, the snail used in this investigation could not rapidly metabolize either DDT or methoxychlor and accumulated both to high levels.

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age 437, Figure 3	Should have caption from Fig. 5, page 440
age 439, Figure 4	Should have caption from Fig. 3, page 437
age 440, Figure 5	Should have caption from Fig. 4, page 439
age 441, Figure 7	Caption should read: The colony on the righ was exposed to constant light for 14 days, while the colony on the left was maintaine in the dark for the same period.

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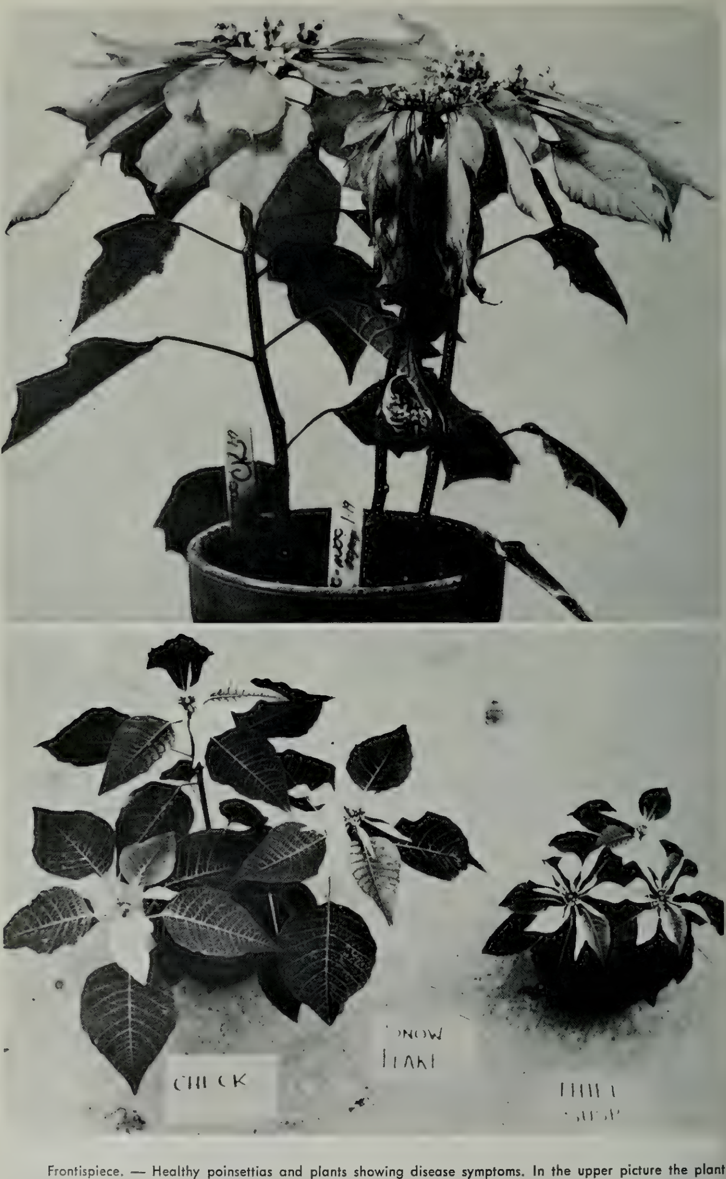

Frontispiece. — Healthy poinsettias and plants showing disease symptoms. In the upper picture the plant in front was inoculated with *Thielaviopsis basicola* when about 90 days old by the stem-incision method. It shows the curling and browning of leaves and the loss of leaves resulting from the disease caused by this fungus. The other plants were not inoculated and remained healthy. In the lower picture the stunted plants on the right were inoculated with *T. basicola* when about 30 days old by the soil-probe method. The control plants on the left were not inoculated and show normal, healthy growth.

A Comparative Study of Two Components of the Poinsettia Root Rot Complex

Robert S. Perry

THE MOST IMPORTANT pathological problem encountered by commercial growers of poinsettias (*Euphorbia pulcherrima* Willd.) is caused by a complex of fungi composed of *Thielaviopsis basicola* (Berk. & Br.) Ferr., *Rhizoctonia solani* Kuhn, and *Pythium ultimum* Trow. Collectively these three organisms cause a condition referred to as the poinsettia root rot complex. Each of these fungi is capable of producing a disease, or they may occur in combination, producing a disease complex. *R. solani* and *P. ultimum* generally attack young poinsettia cuttings during the early stages of propagation, and early death usually occurs. Symptoms of the disease caused by *T. basicola* usually appear later in the season, often near poinsettia marketing time, resulting in root deterioration and leaf drop. The presence of symptoms of any of the diseases caused by these fungi is not restricted to a specific phase of the plant's life cycle but may appear anytime. Since the three pathogens involved respond differently to fungicides and environmental conditions, control of this complex is difficult.

T. basicola is restricted to attacking the roots of poinsettias, but it is capable of producing infection at almost any point on the roots. An extreme infection may cause the entire root ball to turn black and deteriorate. An advanced symptom of Thielaviopsis root rot is a longitudinal splitting of the stem near the ground line. *P. ultimum* commonly produces infection sites near the root tips and causes extensive root deterioration. In the later stages of the disease caused by this fungus, its effects and those produced by the *T. basicola* disease are indistinguishable. *R. solani* attacks poinsettias either at the ground line or at the transition region between the roots and stem. A ground-line infection usually produces girdling of the stem. An infection at the root-stem transition region usually spreads downward through the root system and results in dead and decaying roots with intact white tips, a condition distinguishable from the other two root rots.

It has been shown that each fungus in this disease complex is strongly influenced by soil temperature (Bateman & Dimock 1959). Thielaviopsis root rot is favored by the 13° to 26° C. and Pythium root rot by the 13° to 21° C. temperature range. Although these two diseases are restricted by higher temperatures, Rhizoctonia root rot is favored by the 21° to 30° C. range. The temperature ranges favorable to these three pathogens coincide with the temperatures favorable to growing poinsettias. Therefore, poinsettias are susceptible to one or more members of the complex at all temperatures suitable for poinsettia growth.

Soil pH appears to have as much influence on the development of the disease complex on poinsettias as has temperature. Thielaviopsis (Bateman 1960) and Pythium (Bateman 1962) root rots are most destructive in alkaline, neutral, and slightly acidic soils, but they are considerably restricted in highly acidic soils. Soil pH, however, appears to have little, if any, influence on Rhizoctonia root rot (Bateman 1963).

The diseases caused by these fungi usually have been investigated individually rather than as a complex. Because of the complications involved in working with three pathogens that frequently occur in different population ratios, obtaining consistent, meaningful data for the complex is difficult. Controls have been found for *P. ultimum* and *R. solani* (Tompkins & Middleton 1950; Raabe & Hurlimann 1970). Although a control has recently been suggested for Thielaviopsis root rot of poinsettias (Manning et al. 1970), a single control for the entire complex has not been found.

Since more research has been conducted on *P. ultimum* and *R. solani* than on *T. basicola,* the present research was originally designed to investigate some of the environmental factors affecting the growth of *Thielaviopsis* and the development of the root rot caused by it. However, another fungus, *Chalaropsis thielavioides* Peyronel, frequently was obtained in isolations from diseased greenhouse poinsettias. Since *C. thielavioides* had not been reported as being a part of the poinsettia root rot complex, the author decided to investigate its importance as a pathogen on poinsettias. Numerous similarities between *C. thielavioides* and *T. basicola* were evident. The object of this work was to compare the two fungi. Prior to undertaking such a study, the pathogenicity of *Chalaropsis* on poinsettias had to be established. A comparison of *Chalaropsis* and two isolates of *Thielaviopsis* was made to determine the effects of environment on the growth of the fungi and the ability of the two fungi to produce disease symptoms on poinsettias.

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LITERATURE REVIEW

Thielaviopsis basicola (Berk. & Br.) Ferraris is pathologically important as a member of a root rot complex and as the fungus responsible for the black root rot disease and the internal collar rot disease on more than 120 species of plants in 30 families. *T. basicola* has been reported as a component of a root rot complex on poinsettia (Baker, Davis, & Thomas 1953; Bateman 1962 and 1963; Bateman & Dimock 1959; Dimock 1951; Keller 1954; and Keller & Shanks 1955), citrus (Tsao & Van Gundy 1962), tobacco (Allison 1938;

Stover 1950), and cotton (Blank, Leyendecker, & Nakayama 1953; King & Presley 1942; Leyendecker 1952; Presley 1947; Sherbakoff 1940; and Staffeldt 1959). *T. basicola* is known to produce a root and crown rot on phlox (Peterson 1967). Keller & Potter (1954) have reported that *T. basicola* causes a general root decay of cyclamen, begonia, scindapsus, cineraria, and gerbera. Lloyd & Lockwood (1961 and 1963) reported this fungus on the roots of peas and beans. Ostazeski (1966) reported the stunting and death of bird's-foot trefoil resulting from root-deterioration caused by *T. basicola.*

The influence of various environmental factors on the growth of *T. basicola* in culture and the incidence of disease produced by this fungus have been studied extensively. Bateman (1963) suggested that pH is probably the most influential factor affecting the growth of the pathogen and definitely the most important factor affecting disease development. He reported that *Thielaviopsis* grew best in a range of pH 4.7-5.5 and that cultural growth was retarded on neutral or alkaline media. All of the reports indicate that *Thielaviopsis* is favored by a slightly acid condition. Lucas (1955) found pH to be more influential on the growth of the pathogen in culture than in soils and reported a pH range of 3.9–6.2 for the two media. Keller (1954) found the optimum pH range to be 6.2–7.2 for disease development on poinsettias.

Earlier findings by Rawlings (1940) do not agree with Bateman's suggestions on the importance of the pH factor. Rawlings found pH to exert little influence on the colony type. He reported that pH had a greater influence on the amount of growth (based on colony diameter) than on the colony type or components of the colony. Rawlings also stated that growth on basic agars (pH 7.0–8.0) was greater than growth on acidic agars (pH 4.0–5.0). More chlamydospores were produced on acidic agars than on basic agars.

The effect of temperature on the growth of *Thielaviopsis* in culture and on the development of the disease brought about by this organism have been studied by numerous investigators. Lucas (1955) and Tsao & Van Gundy (1960) reported that the best growth of the fungus in culture occurred at 21° to 28° C. Bateman & Dimock (1959) reported 21° to 24° C. the optimum temperatures for growth. King & Presley (1942) found the best growth to occur at 30° C., whereas an early report by Rawlings (1940) stated that *Thielaviopsis* grew better at 20° C. than at either 10° or 30° C.

Optimum temperatures for disease development are reported to be slightly lower than optimum temperatures for the growth of this fungus in culture. Peterson (1967) declared 16° to 20° C. to be the optimum range for the development of the disease. In this temperature range stem lesions developed in 4 weeks. At slightly higher temperatures lesions developed after 8 weeks. Keller & Shanks (1955) determined the approximate optimum temperature for disease development to be 10° C. Several researchers have attempted to correlate average soil temperatures with soil types in predicting the incidence of disease (Baker, Davis, & Thomas 1953; Bateman 1963; Johnson & Hartman 1919; and Staffeldt 1959). As a result of their work, it is known that certain types of soils are more conducive to Thielaviopsis root rot than are others.

There are few reports on frequency of occurrence of Thielaviopsis root rot in a field situation. Presley (1947) reported that in one field of cotton in Mississippi 20 percent of the plants were killed by *T. basicola.*

Reports in the literature concerning the pathogenicity of *Chalaropsis thielavioides* and the incidence of the disease it causes are scant. This fungus has been reported as a pathogen on the roots of roses (Baker 1953), walnut trees (Hamond 1935), Chinese elms (Wright 1942), agave (De La Isla 1962), and lupine (Longree 1940). In general, *Chalaropsis* has been reported as a fungus that causes the failure of bud and graft unions. Often referred to as the "black mold fungus," *Chalaropsis* frequently produces a fungal mat over the cut surface of the stock to be used in a graft. The impeding presence of the mycelial mat prevents the successful fusion of the stock and scion. Other accounts contain reports of black mold causing grafting failures on roses (Baker & Thomas 1946; Longree 1940; and Milbrath 1946). Baker & Thomas (1946); Lamb, Wright, & Davidson (1935); Wright (1942); and Hamond (1935) stated that *Chalaropsis* is a wound parasite.

Studies on the effect of environmental factors are lacking. Baker & Thomas (1946) reported that the optimum temperature range for growth of *Chalaropsis* in culture was 18° to 30° C.

Boerema (1959) suggested that *C. thielavioides* is an occasional surface contaminant on carrots packaged in perforated polyethylene bags. Lloyd & Lockwood (1962) reported *Chalaropsis* to be a common contaminant on packaged carrots. Since carrot slices are used as an isolating medium for obtaining *Thielaviopsis* from diseased tissues, they warned against mistaking the contaminant *Chalaropsis* for *Thielaviopsis*. Longree (1940) reported numerous similarities between *Chalaropsis* and *Thielaviopsis*. She prepared a good morphological description of *Chalaropsis* and compared several of the different isolates reported prior to 1940.

MATERIALS

Fungi

Two isolates of *Thielaviopsis basicola* were used for testing the effects of environmental factors on the growth and pathogenicity of the fungus. One strain, referred to in this paper as TBT, was obtained from Dr. Peter Tsao of the University of California at Riverside. This culture had been isolated from citrus roots. A second isolate, TBB, was received from Dr. D. F. Bateman of Cornell University. This culture had been isolated from tobacco and was known to be pathogenic on beans also.

A culture of *Chalaropsis thielavioides* was isolated while attempting to isolate *T. basicola* from diseased poinsettias exhibiting symptoms like those of a Thielaviopsis infection. Stock cultures were made by making single-spore isolations from the original cultures. They were maintained in culture by repeated transfer.

Since *C. thielavioides* has been reported to be a contaminant on packaged carrots (Boerema 1959; Lloyd & Lockwood 1962), the *Chalaropsis* may have come from the diseased poinsettia roots or from the carrot slices used as the isolating medium. A check was made on the isolation technique in an attempt to locate the source of the *C. thielavioides*. From every package of carrots used, several sterilized carrot slices were placed in petri dishes. These petri dishes were exposed to the same conditions as were the dishes in which pieces of diseased poinsettia roots had been placed on sterilized carrot slices. *Chalaropsis* was never found on any of the carrot slices that had not been brought into contact with diseased poinsettia root material. In every instance in which *C. thielavioides* grew on the carrot slices, a piece of root tissue was present. Consequently, the fungus must have come from the diseased poinsettia roots.

Media

Several media were used in an attempt to find the most suitable medium for the growth of the two fungi. Commercially prepared Difco media used were lima bean agar, prune agar, malt agar, cabbage infusion agar, cornmeal agar, Noble agar, and potato-dextrose agar. Freshly prepared potato-dextrose agar and carrot-dextrose agar were also used in growth tests. Six media were prepared from living poinsettias. These poinsettia media consisted of leaf-and-stem-dextrose agar, root-dextrose agar, and entire-plant-dextrose agar. The remaining three were of the same components without the dextrose.

Six flowering poinsettias, each approximately 30 cm tall, were cut between the upper root and lower stem regions in preparing the root agar and the leaf-and-stem agar. The root sections were first thoroughly washed and then macerated in a Waring Blendor with 400 ml of distilled water for 5 minutes. The macerated material was added to 1,600 ml of distilled warm water in which 40 grams of agar had been dissolved. This volume was then divided into two 1-liter portions. Twenty grams of dextrose were added to one 1-liter portion of the mixture. This medium was autoclaved at 121° C. for 45 minutes and then poured into petri dishes. The leaf-and-stem agar was similarly prepared, except that the aboveground portions of six poinsettia plants were used. The entire-plant agar was prepared in the same way, except that the medium contained both the roots and the aboveground portions of the plants.

Two broth cultures were used to test growth on a liquid medium. Potato-dextrose broth and V-8 juice broth were made in the same manner as the counterpart agars were made, except that the agar ingredient was omitted. Into 125-ml flasks were poured 100 ml of each broth. The flasks were plugged and sterilized. Seeding was done by dropping fungus plugs into the broth.

Poinsettias

Nine varieties of poinsettias, Barbara Ecke Supreme, Elisabeth Ecke, Mikkel Pink, Mikkel Dawn, Paul Mikkelsen, Stop Light, Snow Flake, Snow Cap, and Ecke White, varying in flower color from dark red, to pink, to white, were used in establishing and maintaining the pathogenicity of *Chalaropsis thielavioides* and *Thielaviopsis basicola*. Six of the varieties were varieties marketed commercially and three were experimental varieties.

METHODS

Microscopic Examinations

Samples of the fungi were obtained by cutting plugs from colonies on agar and by making needle scrapings of diseased host tissues. Microscopic examinations of the fungi were made with a phase microscope. When samples containing only endoconidia were desired, a petri dish containing a fungus colony on agar was flooded with distilled water and slightly agitated. Drops of the liquid containing the spores were then removed from the dish and placed on microscope slides. Needle scrapings of host tissues were placed in drops of lactophenol on slides. The scrapings were usually composed of both mycelium and spores. Measurements of the fungus structures were made.

pH Studies

A pH range was prepared by altering the components of fresh potato-dextrose agar and V-8 juice agar. Two solutions were prepared: a 25-percent lactic acid solution (pH 2.0) and a sodium hydroxide solution made by dissolving 4 grams of sodium hydroxide in 1 liter of water (pH 12.0). A recorded number of drops of these solutions was then added to each of a group of sterilized petri dishes. Basic media were prepared by adding 5, 10, 15, or 20 drops of the sodium hydroxide solution to petri dishes, each of which contained 20 ml of liquified potato-dextrose agar or V-8 juice agar. The dishes were swirled to insure uniform distribution of the solution and the media. Readings of the pH values were taken with a Beckman pH meter before the seedings and after 10 days of growth. The media, after the addition of the sodium hydroxide solution, varied from pH 5.7 to 9.2.

The lactic acid solution was added in portions of 1, 3, 5, 8, 10, or 20 drops to dishes containing 20 ml of V-8 juice agar. These media, after the addition of the lactic acid, had a pH range of 7.1–2.7. The agars were solidified and the dishes then inverted to prevent moisture condensation on the petri dish lids.

Tests on the influence of pH on the growth of the isolates were made on samples of the two fungi grown on V-8 juice agar and potato-dextrose agar. These groups consisted of the various pH plates seeded and kept in constant darkness. The plates were maintained in an incubator at a constant 24° C. Diameters of the colonies were measured every 24 hours for 10 days. Each plate was seeded with a plug approximately 2 mm square taken from actively growing areas in stock culture plates. Three replicate samples of each isolate were tested at each pH level.

Temperature Studies

Seeded plates of standard V-8 juice agar were placed in unlighted incubators set at 5°, 10°, 15°, 20°, and 30° C. Linear growth was measured directly along a consistent diameter bisect every 24 hours for 13 days. Three plates of each of the three isolates at each temperature were measured.

Light Studies

Each of six V-8 juice agar plates was seeded with a plug of TBB isolate, six with a plug of TBT isolate, and six with a plug of *Chalaropsis*. Three plates seeded with TBT, three with TBB, and three with *Chalaropsis* were placed in an unlighted incubator at 24° C. The remaining three plates of each isolate were placed at 24° C. in an incubator lighted by a constant light source of 95 footcandles. Daily measurements of the diameters of the growing colonies were made. Samples were taken from the fungal colonies on the 2nd, 7th, 10th, and 14th days of the testing period for microscopic observation.

Placed in each of thirty-six 125-ml flasks were 100 ml of potato-dextrose broth. In another thirty-six 125-ml flasks were placed 100 ml of V-8 juice broth. For each isolate, 12 flasks of potato-dextrose broth and 12 flasks of V-8 juice broth were used. Eighteen flasks of each broth type were seeded and wrapped in a double layer of aluminum foil. Nine wrapped flasks of each broth were placed on a 144-revolutions-per-minute shaker. Nine flasks of each broth were seeded, placed on the shaker, and exposed to constant light. The remaining 18 flasks of each broth, 9 wrapped in foil and 9 not covered, were placed in the light but not on the shaker. This experiment was conducted at room temperature. Seedings were made by dropping a 2-mm-square plug from an active colony into the broth. Observations were made every 3 days for 15 days.

Pathogenicity Tests

Nine varieties of poinsettias were used in testing the pathogenicity of the two fungi. Cuttings were rooted in sand and then were potted in a soil composed of equal portions of sand, loam, and vermiculite. Poinsettias in the vegetative and flowering stages were inoculated. The vegetative poinsettias averaged 20 cm in height and were growing singly in standard 4-inch pots. The flowering poinsettias varied from 20 to 50 cm tall. These were grown three plants per three-fourth size, 6-inch diameter pot (a pan).

All poinsettias were maintained in a greenhouse at the University of Illinois Floriculture and Ornamental Horticulture Division. The air temperatures varied from 16.7° to 18.3° C. Soil temperatures varied from 15° to 18.7° C. In one brief experiment, the soil temperatures were raised to the 19° to 25° C. range by regulating the air temperature. The plants were watered twice daily and fertilized once daily with a mixture of equal parts (.68 kg, or 1.5 pounds) of ammonium phosphate and potassium phosphate dissolved in 379 liters (100 gallons) of water. Artificial lighting was not used. Shading was used on exceptionally hot days. Most of the pathogenicity tests were conducted during the winter months.

Inocula of each of the three isolates

were prepared by the following method. Four petri dish colonies of the isolate (including the V-8 juice agar, mycelium, and spores) were added to 1 liter of sterile, distilled water and blended for 5 minutes in a Waring Blendor.

Three different methods of placing the fungi in contact with the poinsettias were used. In the soil-drench method, the suspensions were poured over the soil surface in portions of 50 ml per plant (or 150 ml per pan). After the suspension had soaked in, 100 ml of distilled water were poured over the soil.

A second method is referred to as the soil probe. Prior to drenching the soil with 50 ml of inoculum as in the soil-drench method, the root balls of the poinsettias were probed six times with a handled scoopula. This probing served to break some of the roots. The soil around the check plants was drenched with 50 ml of sterile distilled water in place of the inoculum.

The third method of placing the fungi in contact with the poinsettias involved digging the soil away from the crown area of the poinsettias. The exposed upper root-lower stem region was washed with sterile water; the surface was disinfested with 75-percent ethanol; and it was rinsed with sterile, distilled water. A sterilized scalpel was used to make a 1-cm slit into the pith region of the stem. From an actively growing agar colony, a mass of fungus mycelium and spores was removed with a sterilized transfer needle and transferred into the slit. The slit was then covered with petroleum jelly and the soil was replaced. The lower stems of the check plants were disinfested with ethanol, slits were made, the slits were covered with petroleum jelly, and the soil was replaced.

The success of the inoculations was determined from disease symptoms exhibited by the plants and recovery of the fungi from the plants. Comparisons with check plants with regard to general vigor, leaf fall, chlorosis, dwarfing, premature flowering, lesions, and reduced root growth were considered in evaluating the intensity of the diseases.

Isolations from diseased roots and lower stem lesions were made to recover the pathogens. Although potato and sweet potato slices and non-diseased poinsettia stems and roots were also tried, Yarwood's carrot-slice isolation technique (Yarwood 1946) was the only method successfully used in reisolating the pathogens. Packaged carrots were peeled and sliced into discs 40–70 mm thick. Four of these discs were placed in each sterile petri dish. The dishes were stacked under a bell jar. On top of the stack was placed an open dish containing 10 ml of a gaseous sterilant, propylene oxide (Klarman & Craig 1960). The bell jar was sealed for 24 hours to maintain the concentration of the propylene oxide. The jar was then removed and the unopened dishes were allowed to air for 24 hours to disperse the propylene oxide. Root balls of poinsettias showing symptoms of disease were opened and infected root segments approximately 1 cm long were removed. These segments were surface disinfested by placing them in a 5-percent Clorox solution for 2 minutes and then rinsing them in sterile distilled water. The root segments were placed on the sterilized carrot slices in petri dishes, 10 ml of water were added to each dish, and the dishes were kept on a laboratory table. Daily observations were made for the appearance of fungus growth.

RESULTS

Morphology of *Thielaviopsis basicola*

Thielaviopsis basicola produced both reproductive and vegetative stages abundantly in culture as well as on the host. Characteristically, there were two types of vegetative mycelium (Fig. 1*B*). The most common type was hyaline, thin-walled, and septate. The younger hyphae varied from 1.9 to 2.6 μ wide. In culture under favorable conditions,[1] the hyaline mycelium constituted about 90 percent of the vegetative growth and was relatively dense. A second type of mycelium was found in the older areas of the colony, especially in the center, or on the agar surface below the aerial growth. The older hyphae were wider, 2.6–3.9 μ, with dark brown pigmentation.

Both types of mycelia produced spores. The hyaline mycelium produced endoconidiophores in which endoconidia were produced (Fig. 1*D*). During this investigation, growth under mildly unfavorable conditions resulted in an increase in the amount of thick-walled mycelium. A reduction in the growth of both types of mycelia was caused by intensely unfavorable conditions.

This fungus produced chlamydospores and endoconidia in its reproductive phase. The endoconidia were produced abundantly both on the host and in culture. They were single celled and stoutly cylindrical to barrel shaped with rounded corners (Fig. 1*D*). The cellular contents appeared to vary with conditions. Under favorable conditions they were composed of a thin, hyaline cell wall enclosing granular contents and two conspicuous vacuoles, one in each end of the cell.

Endoconidial cells produced under unfavorable pH or temperature conditions appeared to be inconsistent in contents. In some cases the contents appeared to be entirely granular or entirely vacuolated, while in others the two vacuoles appeared to be the sole constituents of the cells.

Aging of the endoconidia produced a slight change in shape. The ends of the individual cells transformed from flattened with rounded corners to semiovoid. During maturation these cells widened slightly, whereas *Chalaropsis* endoconidia appeared to elongate slightly.

Endoconidia of the *T. basicola* isolate from citrus averaged 7.59 x 2.37 μ (Table 1). The endoconidia of this isolate varied from 4.56 to 13.11 μ in length and from 2.28 to 2.85 μ in width. Mean dimensions of the endoconidia of the isolate from tobacco were 7.96 x 2.85 μ, with a range of 5.20–11.70 μ long and 2.28–3.42 μ wide. Except for these slight deviations in measurements, the endoconidia from the two isolates were identical. Germ tubes developed from the ends of the cells. In this study germ tubes were not observed developing from the middle region of the cell in either *Chalaropsis* or *Thielaviopsis*.

Thielaviopsis endoconidia were indistinguishable from those of *Chalaropsis*. Generally, the biguttulations of *Thielaviopsis* endoconidial cells were more prominent, but this characteristic was not sufficiently consistent to permit separation of the two fungi.

Thielaviopsis endoconidia were produced within endoconidiophores similar to those of *Chalaropsis*. They were composed of tapering terminal cells (phialides) and one to four basal cells. In the isolates of the fungi studied in this investigation, basal cells varied in length from 6.3 to 9.1 μ and averaged 2.6 μ wide. In the *Chalaropsis* isolate the basal cells of individual endoconidiophores frequently varied slightly in size in such a way that the largest cell was at the end opposite the spore-producing cell. There was a progressive reduction in size of the remaining cells toward the terminal cell.

In the two isolates of *Thielaviopsis* this condition occasionally occurred, but usually all of the basal cells were of the same size. This condition made it difficult to distinguish the termini of the hyphae and the origins of the endoconidiophores. However, endoconidiophores arising from short, lateral branches were easy to differentiate. The tapering terminal cells varied in length from 15.6 to 32.4 μ. Endoconidiophores

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[1] Throughout this paper references to unfavorable conditions indicate pH, temperature, or light conditions, individually or combined, that were not conducive to the best growth of the fungi. Favorable conditions are the pH, temperature, and light requirements indicated by this study as being most conducive to the growth of the two fungi.

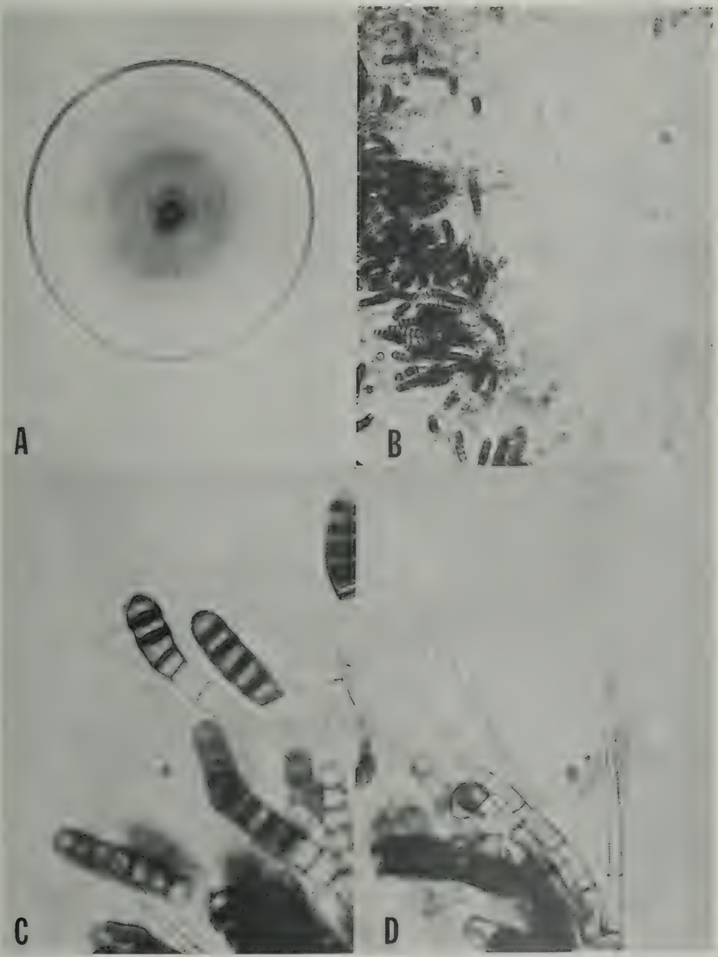


Fig. 1. — *Thielaviopsis basicola: A*, 10-day-old colony on V-8 juice agar; *B*, colony components — two kinds of spores and two types of mycelia (X 130); *C*, chlamydospore chains (X 520); and *D*, endoconidiophores with endoconidia (X 520).

were produced individually or in clusters on terminal tips of hyphae or on stubby lateral branches. Endoconidiophores produced in clusters were of various lengths, because they did not arise from a common point but from various subbasal, hyphal cells.

Conidia were produced endogenously by the phialides of the conidiophore. Although these spore-producing cells produced conidia individually, several conidial cells in different stages of development could be seen within a single conidiophore. Mature cells were extruded singly from the apex. Conidia not dispersed after expulsion from the terminal cells occasionally created chains by adhering to one another end to end. Chains of conidia containing 15 or more cells were observed.

The thick-walled, dark brown, segmented mycelium produced chlamydospore chains. Most of the thin-walled hyphae remained hyaline and did not change. However, some of this mycelium in certain areas of the colony became dark brown, remained segmented, and developed thick walls. The terminal tips of the thicker hyphae developed into single, hyaline, bulbous cells. Other than the enlarged tip, no apparent specialized structures were observed. As the tip cell became more ovoid to elongately ovoid to club shaped, the walls thickened and the entire structure became darkly pigmented. Cross walls developed as the cell elongated to produce a final structure of two to seven chlamydospores (Fig. 1*C*).

One hundred chlamydospores and 100 chlamydospore chains of each isolate, TBT and TBB, were measured (Table 1). Chlamydospore chains of the TBT isolate averaged 20.4 x 5.8 μ. The largest chain measured 28.3 x 7.27 μ and contained seven spores. The smallest chain measured 17.1 x 5.7 μ and consisted of four spores. The mean length of an individual spore was 4.41 μ.

Chlamydospore chains of the TBB isolate averaged 18.2 x 5.7 μ. The largest chlamydospore chain measured 26.0 x 6.5 μ and was composed of six spores. The smallest measured 13.0 x 4.8 μ and was composed of three spores. The individual spores averaged 3.99 μ in length.

Chlamydospore chains were produced at the ends of long strands of hyphae. Clusters of chlamydospore chains were the result of clusters of hyphal strands rather than the branching of a single

Table 1. — Comparative measurements, in microns, of spores of the two isolates of *Thielaviopsis basicola* used in this investigation.

Isolate	*Host*	*Endoconidia*						*Chlamydospore Chains*						*Spores Per Chain*			*Average Length of Spores*
		Length			Width			Length			Width						
		Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	
TBT	Citrus	13.11	4.56	7.59	2.85	2.28	2.37	28.30	17.10	20.40	7.27	5.70	5.80	7	4	5	4.41
TBB	Tobacco	11.70	5.20	7.96	3.42	2.28	2.85	26.00	13.00	18.20	6.50	4.80	5.70	6	3	4	3.99

strand. Mature chlamydospore chains were released from the parent mycelium by fragmentation. The chlamydospore chains were released intact with a short fragment of hypha still attached to the basal cell.

Some controversy has developed among plant pathologists over the germination of *Thielaviopsis* chlamydospores. Christias & Baker (1967) reported that before germ tubes could develop, the individual spores comprising the chain had to be separated. Each spore was then believed capable of germination. Their work appeared to demonstrate the function of chitinase in breaking the spores apart so that germination could take place. However, Papavizas & Adams (1969) later demonstrated that intact chlamydospore chains, as well as individual chlamydospores, were capable of germination. They found that the breaking up of chlamydospore chains into individual spores by chitinase was not a necessary prelude to germination. I did not study the germination of chlamydospores. There is no record of a necessary maturation or resting period before germination of *Thielaviopsis* chlamydospores as has been noted in *Chalaropsis* chlamydospores (Longree 1940).

Colony Characteristics of *T. basicola*

Observations were made and data were recorded on the development of *Thielaviopsis basicola* colonies on V-8 juice agar and potato-dextrose agar. More extensive development of vegetative and reproductive structures occurred on V-8 juice agar. Growth of *T. basicola* on V-8 juice agar was luxuriant but slow. A 15–16 day growth period under favorable conditions was required for both of the isolates studied to completely cover the agar surface in a 90-mm diameter petri dish. However, measurable growth was recorded 2 days after seeding.

The first growth appeared as hyaline, vegetative hyphae radiating outward from the point of seeding. Throughout the development of the colony, the outermost perimeter was composed of these hyaline, nonsporulating hyphae appressed to the agar surface. On the 4th day after seeding, aerial, hyaline mycelia began to be produced around the seeding point and to develop progressively outward. By the 5th day after seeding, endoconidiophores and endoconidia could be found in the aerial hyphae.

Within the next 48 hours the hyphae around the seeding plug began to darken. Microscopic examinations of the fungus in this region revealed that the darkening was brought about by the production of darkly pigmented, thick-walled hyphae. These dark strands predominated the fungal mass but remained close to the agar surface. Pigmentation appeared to vary between dark gray to black and golden brown. Pigmentation did not appear to be consistent with the isolate, as both isolates produced both color types but not within the same colony.

The dark, thick-walled hyphae gave rise to the terminal chlamydospore chains. The chlamydospores were also thick-walled and darkly pigmented in colors corresponding to those of the hyphae from which they had developed. As chlamydospore production continued to increase, endoconidial production decreased.

A fully developed colony consisted of a series of concentric circles of visible differences in growth type (Fig. 1*A*). The innermost region around the point of seeding was a mass of compacted, semi-aerial, dark-walled hyphae. Thick-walled, dark hyphae and chlamydospore chains composed approximately 95 percent of the fungus material in this region, but occasional hyaline hyphae were found. This center region, about 10 percent of the entire colony area, had a black, matted appearance. The next growth ring constituted about 40 percent of the colony area and was composed of approximately 75 percent dark hyphae and chlamydospore chains and 25 percent hyaline hyphae and endoconidia. Because of the presence of fewer dark hyphae in relation to the mass of hyaline hyphae and the more aerial nature of the hyaline hyphae, this region had a gray, wool-like appearance.

In the remaining concentric growth patterns, the percentages of dark hyphae and chlamydospore chains comprising the fungal colony decreased progressively as the distance from the point of seeding increased. The proportion of hyaline hyphae and endoconidia increased progressively as the distance from the seeding point increased. Apparently no standard number of concentric growth rings made up a colony. Common borders between the growth rings were not sharp and well defined but were transition zones gradually integrating one ring with the next. Additional characteristics of typical *T. basicola* colonies observed during this study were consistent with those described by Johnson & Valleau (1935).

T. basicola on Poinsettias

Thielaviopsis endoconidia were found on almost all external surfaces of diseased areas on poinsettias. Abundant endoconidia were found on decaying root segments, in lesions on lower stems, and on the inner walls of the lower pith cavities of the stem. These spores were always found on the external or internal surfaces but never embedded within the host tissue. As did those of *Chalaropsis,* the thin-walled, hyaline hyphae ramified within the infected host tissue. Endoconidiophores developed from the hyaline hyphae that were either on the surface of the host or embedded in the diseased tissues. Endoconidial production seemed to be influenced little by environmental factors or host conditions. Endoconidia were found either on or within the host on internal surfaces at any time when symptoms of *Thielaviopsis* infection were present.

Thielaviopsis chlamydospores were produced much less frequently on the host than were the endoconidia. However, the *Thielaviopsis* chlamydospores were found more frequently on the host than were *Chalaropsis* chlamydospores. Chlamydospore production of *Thielaviopsis* seemed to be related to environmental conditions and the development of the disease. The development of longitudinal lesions on the lower stems of the poinsettia host was a symptom of an advanced stage of *Thielaviopsis* infection. Chlamydospores were found in these lesions. During my investigation, chlamydospores were detected only within the stem lesions, probably because chlamydospore production required light. Masses of thick-walled, darkly pigmented hyphae with multispored, terminal chlamydospore chains developed within these lesions.

Morphology of *Chalaropsis thielavioides*

The vegetative stage of *Chalaropsis thielavioides* consisted of septate hyphae that varied in width from 1.2 to 2.6 μ. In culture most of the hyphae were thin and hyaline. As they aged, the cells became slightly wider, and the walls darkened. The reproductive structures were produced on this type of mycelium. Even under favorable conditions the mycelia were sparse. Most of the growth consisted of endoconidiophores arising from the older hyphae. Under unfavorable conditions the mycelia became even more sparse than that produced under normal conditions. The darkening of the mycelium as it aged varied inversely with the intensity of the unfavorable conditions. Under highly unfavorable conditions the mycelium failed to darken and remained thin walled, and vacuoles predominated the segmental contents. The hyphal cells sometimes enlarged to produce bead-like strands of mycelium.

This fungus produced two types of asexual spores, endoconidia and chlamydospores (Fig. 2*B*). The endoconidia were produced within endoconidiophores (Fig. 2*D*), each composed of two or three basal cells and a spore-producing cell (phialide). The basal cells varied from 6.5 to 9.1 μ in length and were about 2.6 μ wide. The spore-pro-

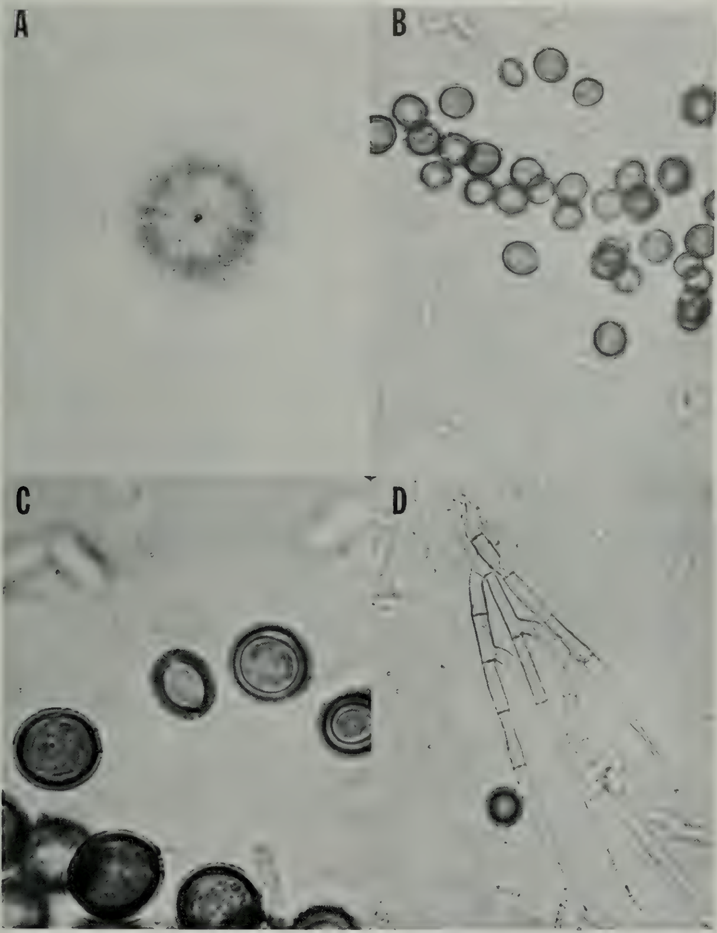


Fig. 2. — *Chalaropsis thielavioides: A*, 10-day-old colony on V-8 juice agar; *B*, components of a typical colony (X 520); *C*, chlamydospores (X 1235); *D*, endoconidiophores with endoconidia (X 520).

ducing terminal cell varied from 11.7 to 27.3 μ in length. The tapered phialides produced endoconidia singly. Although several endoconidia in various stages of formation were seen within a terminal cell, the mature endoconidia were extruded from the apex individually. A stubby side branch occasionally developed from a mature strand of mycelium. One to five endoconidiophores developed from this branch. It was not uncommon to see several conidiophores on one lateral branch (Fig. 2*D*).

The endoconidia of *C. thielavioides*

Table 2. — Comparative measurements, in microns, of spores of Chaloropsis *thielavioides* occurring on and isolated from various host plants.

Authority	Host	*Endoconidia*						*Chlamydospores*					
		Length			Width			Length			Width		
		Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
Peyronel[a] 1916	Lupine	55.0	8.0	. . .	4.5	3.0	. .	20.0	10.0	. . .	15.0	8.0	. . .
Hamond 1935	Walnut	40.0	7.5	14.7	5.5	2.0	3.7	22.0	10.0	16.5	16.0	8.0	12.1
Hamond 1935	Carrot	24.0	9.0	14.2	6.0	3.0	3.6	16.0	11.0	12.9	14.0	10.0	12.1
Longree 1940	Rose	32.6	7.0	9.5	7.4	2.6	3.3	17.0	9.6	13.5	15.4	8.0	11.4
Longree 1940	Chinese Elm	35.4	9.5	14.7	5.1	2.6	3.9	17.6	10.2	14.4	16.0	9.9	12.9
Perry[b] 1969	Poinsettia	13.7	3.4	7.5	2.3	1.1	1.7	8.6	6.3	7.6	8.6	6.3	7.6

[a] Measurements taken from Longree (1940).

[b] Measurements rounded off to coincide with measurements from other investigators.

were produced in great abundance on the host and in culture. These cells were found clinging together in chains of a dozen cells or more. Endoconidia germinated at any time after they were released from the conidiophores. Germ tubes were produced from the ends or the sides of the spores. Individual endoconidia were hyaline and biguttulate. They were barrel-shaped to cylindrical with rounded corners. As these cells aged, the ends became slightly more rounded. The endoconidia varied from 3.42 to 13.68 μ long and 1.14–2.28 μ wide, with mean dimensions of 7.50 x 1.67 μ. The endoconidia of minimal dimensions were almost always found in chains. Spore measurements of the isolate used in this work and the spore measurements of isolates used by other workers are compared in Table 2.

A second type of asexual spore, the chlamydospore (Fig. 2*C*), was produced in fewer numbers than were the endoconidia. Longree (1940) referred to these as macroconidia. These cells were produced only in the older parts of a colony. Short lateral branches developed from cells of the older, pigmented mycelium. The tips of these lateral branches and the terminal tips of the hyphae became bulbous. Longree (1940) reported that macroconidia and macroconidiophores were frequently found clustered at the base of an endoconidiophore. In my investigations I did not find this condition. Macroconidia from the *C. thielavioides* used in this work were always produced individually and not at the bases of endoconidiophores.

Maturing chlamydospores were thin walled and hyaline for a short while, but soon became thick walled and darkly pigmented. The mature chlamydospores were subglobose to ovoid with small flattened bases. Mature chlamydospores were freed from the colony without any portions of the conidiophores still attached to them. Spores freed shortly before maturity often still had a short fragment of conidiophore attached. Freed, hyaline chlamydospores sometimes had a fragment of conidiophore equal in length to several times their diameters.

The diameter of the chlamydospore varied with the isolate. Mature chlamydospores from the isolate used in this investigation were spherical, with a mean diameter of 7.64 μ. They varied from 6.27 to 8.55 μ in diameter. As indicated by the data in Table 2, other reports of this fungus show the chlamydospores to be more ovoid than spherical.

These spores did not germinate readily. None of the chlamydospores observed showed any evidence of germination. However, the cultures were not maintained for more than a month. Longree (1940) stated that the macroconidia either require a resting period or mature slowly. She found that 2-month-old macroconidia germinated poorly, whereas the percentage of germination was greater in 3-month-old spores. Chlamydospores were produced only after the mycelium had reached a certain stage of maturity or when the mycelium was subjected to unfavorable conditions.

Colony Characteristics of C. *thielavioides*

Chalaropsis thielavioides grows luxuriantly on only a few agar media. Although it does grow on most common agars, the fungus sporulates abundantly and produces an extensive colony on only a few. Good growth was produced on V-8 juice-dextrose-yeast extract agar (Fig. 2*A*), but even this growth was slow. On V-8 juice agar *Chalaropsis* covered the agar surface in a 90-mm diameter petri dish in 10–12 days under favorable conditions. If a plug of agar with fungal spores and mycelium was placed on agar in a petri dish, measurable growth was observed after 2 days. This first growth appeared as nonsporulating hyphal strands living on or slightly below the agar surface. The vanguard of hyaline mycelia continued outward, preceding the subsequent colonial development. If a single point of seeding was made on the agar, a circular colony was almost always produced.

For the first few days the colony appeared hyaline, and then it began to whiten. The change to white was brought about by the production of endoconidiophores and endoconidia. These reproductive structures grew with a concentric perimeter slightly (about 5 mm) within the enlarging hyaline perimeter. After 5–6 days of growth under favorable conditions, *Chalaropsis* produced a colony that covered about two-thirds of a 90-mm diameter petri dish. By this time a small, circular halo immediately surrounding the initial plug had turned black. This blackened area consisted of developing and mature chlamydospores. The mycelium was almost entirely on the surface of the agar or slightly submerged, and it was pigmented a golden brown. The black color in the colony was due to the dark-brown-to-black pigmentation of the numerous chlamydospores. Although the mycelium in the chlamydospore area remained on the surface, the surrounding mycelium became more aerial and fluffy. This caused the center area to appear sunken in the white mycelium. After 8–10 days a light gray area constituting about one-half of the colony began to appear in the center of the colony. The gray color was due to the intermingling of maturing chlamydospores and the accompanying abundant endoconidia.

The fully developed colony appeared as a series of progressively lighter colored, concentric circles. The innermost circle, about one-tenth of the total area, was black; sunken; and composed of many chlamydospores, few endoconidia, and much thick-walled mycelium.

The next zone was fluffy and whitish gray and accounted for about one-half of the colony area. This area consisted of abundant endoconidia, much thin-walled mycelium, and abundant chlamydospores. When this area was scraped from the agar and the surface of the agar was examined, a dark surface growth of thick-walled mycelium was seen radiating outward from the center. This surface growth appeared to terminate after enlarging to about one-half of the area of the entire colony. Chlamydospores which grew up through the aerial endoconidial mycelium and caused the graying of this region were produced from this growth.

The next outermost circle was white and, although definitely aerial, not quite as fluffy as the adjacent, inner region. This white area constituted about one-third of the colony and was composed almost entirely of endoconidia, endoconidophores, and thin-walled hyphae. The surface growth below this region frequently was grayish and contained few chlamydospores.

The outermost concentric region made up about one-tenth of the total area. It consisted entirely of surface and subsurface, hyaline, thin-walled hyphae with no spores of either type. Under ideal conditions, the margin of the colony was regular. Abnormal or adverse conditions frequently produced lobed or irregular margins. A 10-day-old *Chalaropsis* colony on V-8 juice agar grown under favorable conditions is shown in Fig. 2*A*.

C. thielavioides on Poinsettias

Signs of *Chalaropsis* were more difficult to find on the poinsettia plant than were signs of *Thielaviopsis*. *Chalaropsis* endoconidia were found in moderate numbers on the external surfaces of the diseased areas of the roots. These spores were also found externally in the areas of the stem where bark had been loosened or sloughed off near the ground line. All of the mycelium produced within the infected host tissues was thin walled and hyaline. This mycelium was difficult to locate in the decaying tissues. It appeared to produce endoconidiophores that protruded through the epidermis of the host tissue and extruded the endoconidia externally.

Chlamydospores of *Chalaropsis* were

not produced abundantly on poinsettias. Environmental conditions or host influence may have been responsible for the lack of abundant chlamydospores. Chlamydospores from the isolate used in this experiment were found only in the pith cavities of the lower stem region of the host. These spores appeared to be restricted to the lowest pith chamber, since they were not found in the upper chambers of the stem. Thick-walled, darkly pigmented hyphae developed on the walls and septations of the lowest chamber. Individual terminal chlamydospores were produced from the thick-walled hyphae. No chlamydospores were found embedded in the host tissues, on diseased roots, or on any diseased surface exposed to light. Light may have been the critical factor that determined the location of *Chalaropsis* chlamydospore production.

Comparison of Growth of *Chalaropsis thielavioides* and *Thielaviopsis basicola* on Various Media

Various media were tested to determine the one most satisfactory for culturing the three isolates. Of the media tested, V-8 juice agar was the most satisfactory. Prepared as suggested by Miller (1955), this agar had a pH range of 7.0–7.25. Both fungi produced vegetative and reproductive structures abundantly on this medium.

Both fungi grew and sporulated equally well on carrot-dextrose agar and V-8 juice agar, but the carrot-dextrose agar was not used because of its more involved method of preparation. V-8 juice can be easily purchased, whereas carrot juice is not so readily available. A juice was easier to use in the media preparation than macerated carrot tissue.

Potato-dextrose agar was not as satisfactory as the V-8 juice agar. Hyaline mycelia and endoconidia were produced on potato-dextrose agar, but chlamydospores and dark hyphae were produced infrequently and sporadically. Colonies of both fungi on potato-dextrose agar were sparse and usually occurred below the surface or appressed to the surface.

Testing of the poinsettia agars proved interesting but not too beneficial. No growth was made by either fungus on agar derived from poinsettia tops only, either with or without dextrose. Growth of *Thielaviopsis* on agar derived from the entire poinsettia plants was poor. This growth consisted of light gray, random mycelia on the agar surface. Sporulation did not occur. *Chalaropsis* produced a sparse, aerial mycelium with some endoconidia. Again, the presence or absence of dextrose had little effect. All three isolates grew well on the poinsettia-roots-only agar. Both types of vegetative and reproductive structures were produced abundantly. Growth of all three isolates was noticeably better on the dextrose-supplemented agar. Fungal growth on these two media was comparable to growth on V-8 juice agar. The poinsettia-roots medium was not used, however, because of the extra time and effort required in its preparation.

Growth on lima bean agar, prune agar, malt agar, cabbage infusion agar, cornmeal agar, and Noble agar was negligible. Of all the agars tested, only potato-dextrose agar and V-8 juice agar were used in subsequent experiments.

Two liquid media were tested. Potato-dextrose broth and V-8 juice broth supported good growth of both fungi. *Chalaropsis* produced a complete surface mat in 7 days on V-8 juice broth. *Thielaviopsis* produced a complete mat in 10 days. Both fungi failed to produce a complete mat on potato-dextrose broth.

Neither fungus produced any growth in either of the two broths in shake cultures.

Comparison of Growth Rates

Daily measurement of the colonial enlargement of the three isolates indicated that *Chalaropsis* was the fastest growing. The colony increased at the rate of 8.0 mm in diameter per day. The colony produced was dense and contained both coarse and fine hyphae as well as both types of spores.

The colonies of both isolates of *Thielaviopsis* increased 5.9 mm in diameter daily. This fungus grows somewhat slower than *Chalaropsis*. The colonies produced were similar to those produced by *Chalaropsis*. They were dense and contained both types of hyphae and both types of spores. The rate of growth of each isolate is shown graphically in Fig. 5.

Effect of pH

Although temperature influenced the amount of growth, pH influenced the type of growth of the fungi reported on here. Conspicuous variations in the morphology of the fungi accompanied variations in the pH of the media. Fig. 3 shows the effect of pH on colony growth.

C. thielavioides had a narrower favorable pH range than either isolate of *T. basicola*. *C. thielavioides* produced some growth at pH 3.9 and fair growth at pH 9.2. In my opinion, based on the amount of growth and quality of the colony, the optimum pH range for *Chalaropsis* was 6.7–8.0 (Fig. 3*A*). Although colonies on agars with a pH in excess of 8.0 produced normal daily colonial enlargement, the hyaline hyphae were distorted in shape and the endoconidia were nearly oval. An increase in pH to above 8.0 produced an intensification of the distortions. Chlamydospores and dark hyphae were sparse or absent in all colonies on agar with a pH greater than 8.0. Colonies on agars with a pH between 8.0 and 8.7 were appressed to the agar surface. Colonies on agars with a pH higher than 8.7 were almost entirely submerged and definitely hyaline.

Chalaropsis grew better on basic agar than on acid agar. Although the growth of reproductive and vegetative structures was retarded on agars in the lower pH range, the deforming of structures was not as extensive as it was on the basic agars. Growth was reduced on agars with a pH of less than 7.0. Colonies varied from dark gray at pH 6.8 to whitish gray at pH 3.8. On none of the acidic agars did the colonies appear hyaline. Their color was due to the dark, thick-walled hyphae intermingled with some hyaline hyphae and endoconidia. At the lower end of the pH range, there were fewer chlamydospores. The colony produced at pH 3.8 contained occasional thick-walled hyphae but no chlamydospores. An abundance of endoconidiophores was responsible for the whitish color of this colony.

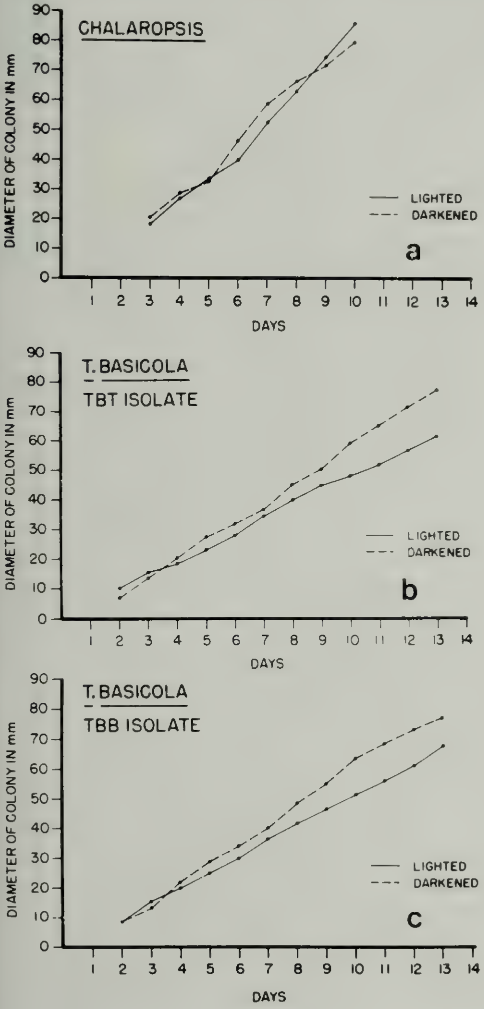
The type of growth also varied as pH values varied. A decrease in pH produced an increase in the mass of aerial hyphae. Colonies on highly acidic agars appeared fluffy in comparison with the wooly colonies grown at pH 7.0.

Variations in pH influenced the growth of isolate TBT more than that of isolate TBB. Neither isolate grew at a pH lower than 3.2. Although the basic limit was not defined, a progressive decline in the growth and formation of typical structures of the colonies at pH 9.0 indicated that the maximum was somewhere near that point. As Fig. 3*C* shows, after 10 days of growth the diameters of TBB colonies on agars with various pH values ranged from 18 to 62 mm. A variation of 27–74 mm in the diameters of the TBT isolate colonies occurred on these agars (Fig. 3*B*). The optimum for both isolates was between pH 5.9 and 6.7. The colonies on agars outside of the optimum pH range produced more vegetative structures than reproductive structures.

TBB and TBT colonies on agars within the optimum pH range were white for the first 2–3 days, due to the abundant production of thin-walled hyphae and endoconidiophores. After several days the colony, except for a narrow white perimeter, developed shades of gray. The gray color resulted from the production of chlamydospores and thick-walled hyphae. Daily diameter enlargement varied between 5.8 and 7.4 mm.

Morphologically, the colonies on the

more basic media tended to be light gray to whitish. As the basic condition was intensified, chlamydospore production was lessened and endoconidial production became greater. At pH 8.0 the colonies of both isolates consisted almost entirely of masses of endoconidiophores with few other structures. These colonies were characterized by alternate rings of dense and sparse masses of endoconidiophores. Occasionally chlamydospores and some dark hyphae were



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front cover

Fig. 3. — The effect of variations in pH and medium type upon the growth of: *A, Chalaropsis thielavioides; B,* the TBT isolate of *Thielaviopsis basicola; C,* the TBB isolate of *T. basicola.*

observed in random clumps, usually within the denser mycelial circles. Colonies of both isolates of *Thielaviopsis* on agar with a pH value of 8.6 were composed almost entirely of hyaline hyphae appressed to the agar surface. A few endoconidia were present. Each colony on agar more basic than pH 8.6 consisted only of thin, distorted, hyaline hyphae embedded in the agar. The daily diameter growth of the colonies growing on media with pH values above 6.7 varied from 3.6 to 6.5 mm.

Acid media induced the formation of a different type of colony. Each colony on an acid agar was composed mainly of aerial mycelium. Concentric circles within the colony were produced on agars with pH values of 7.0–4.5. However, the mycelium in each of these circles was black to intermediate gray. Growth on media with a pH as low as 4.5 resulted in an increase in the production of chlamydospores. This increase produced a corresponding darkening of the colonies to almost entirely black.

Colonies of both isolates grown on agars in the pH range 4.5–4.1 were lighter in color than colonies on slightly less acidic agars. Chlamydospores and dark hyphae were produced in clumps. They were not produced on strongly acidic agars. No chlamydospores were produced on agars with pH 3.7 or below. Fluffiness (or the amount of the aerial mycelium) increased as the pH of the agar decreased down to pH 3.7. Colonies on the pH 3.7 agar were almost entirely aerial and composed of elongated strands of hyaline hyphae. A few endoconidia and endoconidiophores were found. Colonies on these highly acidified agars were dense enough to form visible margins. These margins were characteristically reticulately lobed. Margins of colonies produced on the highly basic agars were characteristically smooth. Daily increases in diameters of the colonies on acid media varied from 1.8 to 6.2 mm. Both isolates of *Thielaviopsis* failed to grow on agars with a pH of 3.2 or lower.

The effect of fungus growth on the pH of the media was not determined. Before the agar plates were seeded, the pH was adjusted by adding a predetermined number of drops of acid or base solution to the liquified media. After the 10-day testing period, the media were remelted and tested for pH with a pH meter. The changes in pH of most media were so slight as to be negligible. Fluctuations that may have taken place during the 10-day period were not determined.

Effect of Temperature

Temperature exerted an effect on the rate of growth but not on the type of growth of the fungi reported on here. In all tests where temperature did not severely restrict growth, the three isolates produced colonies characterized by a dense composite of both types of hyphae and both types of spores. The only variation was in the diameters of the colonies.

As shown in Fig. 4*A*, the greatest amount of growth of *Chalaropsis* occurred at 30° C. Daily enlargement of colonies growing at this temperature varied between 6.4 and 8.5 mm. An abrupt decrease in growth at 35° C. resulted from the thermal death of many mycelial cells. Although growth at 10° C. was slight, it was measurable and averaged about 1.2 mm per day. Growth was evident at 5°C.; however, it was restricted to the seed plug and too limited to be measured.

The optimum temperature for growth of both isolates of *Thielaviopsis* was 25° C. (Fig. 4*B* and *C*). The TBB isolate grew slightly better at 30° C. than did the TBT isolate. Colonies maintained at 20° C. and 15° C. produced both types of spores and both types of hyphae but were smaller than the colonies grown at 25° C. The TBT isolate produced no growth at either 5° C. or 10° C. TBB, however, produced visible growth at 10° C., but it was confined to the seed plug and was too limited to be measured. This isolate produced no growth at 5° C.

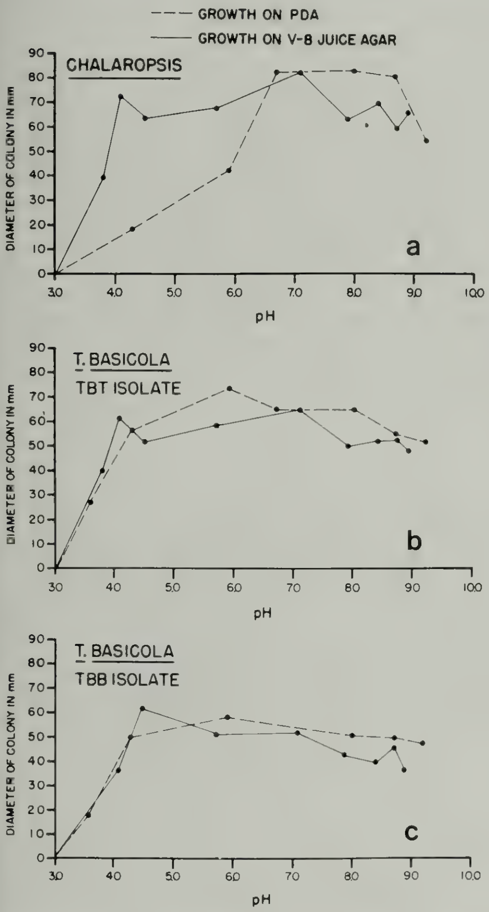

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Fig. 4. — The effect of temperature upon the growth of: *A, Chalaropsis thielavioides; B,* the TBT isolate of *Thielaviopsis basicola; C,* the TBB isolate of *T. basicola,* all on V-8 juice agar.

Effect of Light on Growth Rates

As shown in Fig. 5*A*, *Chalaropsis* grew slightly more rapidly in the light than in the dark. While the growth of the colony in the light averaged 8.6 mm in diameter per day for a 10-day period, the growth of the colony in the dark averaged only 8.0 mm per day. During the first half of the test period, growth in the dark slightly exceeded growth in the light. Numerous chlamydospores were produced in the dark after 7–10 days, after which mycelial growth was retarded (Fig. 6). Since few chlamydospores were produced in the light, mycelial production was not noticeably retarded. Microscopic examination of the colonies after 14 days revealed that the colony grown in the light consisted mainly of hyaline hyphae and endoconidia. The colony grown in the dark

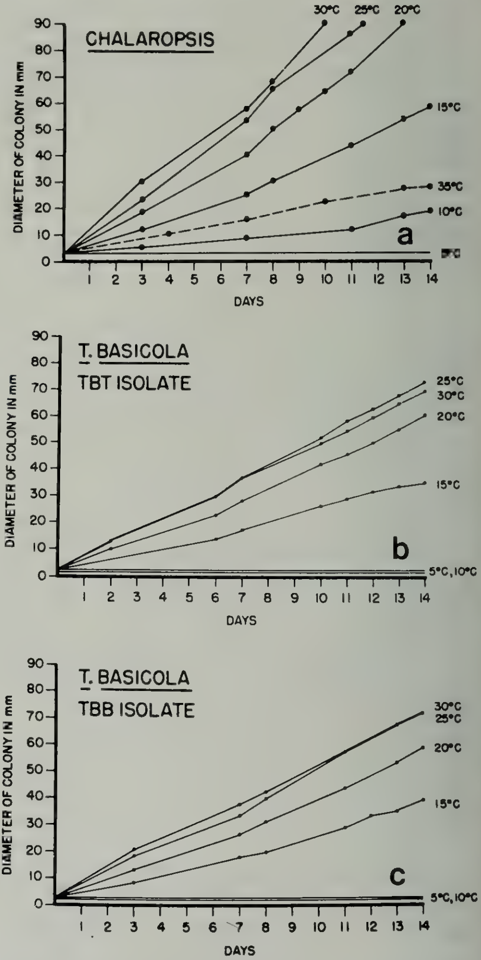

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Fig. 5. — The effect of light upon the growth of: *A*, *Chalaropsis thielavioides*; *B*, the TBT isolate of *Thielaviopsis basicola*; *C*, the TBB isolate of *T. basicola*, all on V-8 juice agar.

was generally darker gray and composed of thick-walled, dark hyphae and chlamydospores as well as hyaline hyphae and endoconidia.

Both of the *Thielaviopsis* isolates produced more growth in the dark than in the light (Fig. 7). The TBB isolate averaged 5.9 mm of diameter growth per day in the dark and 5.2 mm per day in the light. As Fig. 5C shows, growth in the dark was consistently greater than growth in the light. Production of chlamydospores and dark-walled hyphae seemed to be favored by light. Fourteen-day-old colonies grown in the light contained many more chlamydospores and dark hyphae than the colonies grown in the dark. These

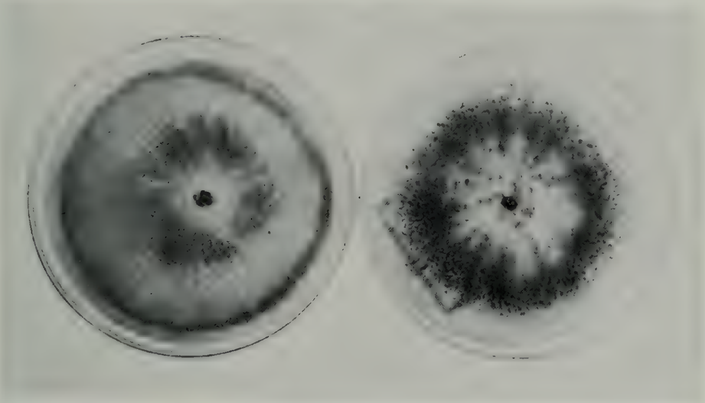

Fig. 6. — The effect of light on colony development of *Chalaropsis thielavioides* grown on V-8 juice agar. The colony on the left was exposed to constant light for 14 days, while the colony on the right was maintained in the dark for the same period.

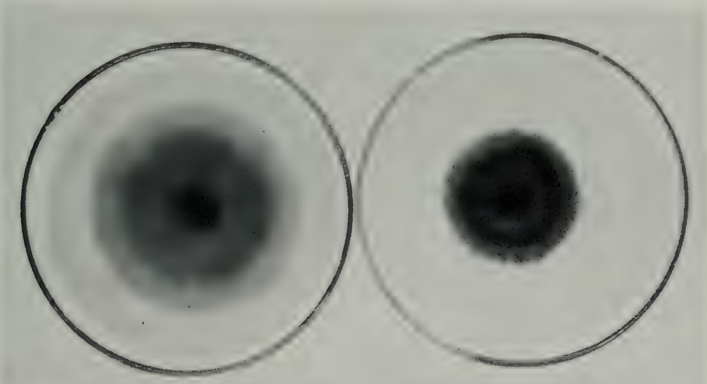

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Fig. 7. — The effect of light on colony development of *Thielaviopsis basicola* grown on V-8 juice agar. The colony on the left was exposed to constant light for 14 days, while the colony on the right was maintained in the dark for the same period.

two structures were evident in the 2-to-3-day-old lighted colonies, which produced chlamydospores and dark hyphae throughout the test period. The *Thielaviopsis* colonies produced under light were dark gray to black; the colonies produced in the dark varied from dark gray through light gray to whitish.

Colony color, morphology, and other characteristics of TBT and TBB isolates of *T. basicola* grown in the light were almost identical, as were the characteristics of the same isolates grown in the dark. Apparently the reaction to light is a characteristic of the fungus rather than of the individual isolates. Like the

TBB isolate, the TBT isolate averaged 5.9 mm of daily diameter growth in an unlighted situation. Light appeared to be more influential in retarding the growth of TBT than in slowing that of TBB. The diameter growth of TBT cultures in the light averaged only 4.7 mm per day. The average rates of growth of these colonies are shown in Fig. 5*B*.

Colony components, growth rate, and growth type of the *T. basicola* isolates when grown on liquid media in the light were comparable to those produced on agar media in the light. Likewise, the colonies grown on liquid media in the dark were similar to those grown on agar media in the dark. Although direct measurements of growth were not made, daily observations and frequent microscopic examinations were used to observe the development of the isolates. Growth on lighted and unlighted potato-dextrose broth was not as profuse as growth on V-8 juice broth. *Chalaropsis* produced more chlamydospores and thick-walled hyphae in unlighted cultures. Both isolates of *Thielaviopsis* produced abundant chlamydospores and thick-walled hyphae in the lighted cultures. In all cases the three isolates produced limited amounts of hyaline hyphae and endoconidia within the liquid and profuse amounts on the surface. The production of chlamydospores and dark hyphae was limited to the surface mat.

Results of Pathogenicity Tests

Evaluations of the success of the infection tests were based on these criteria: (i) production of external and internal disease symptoms on or in the host plants, (ii) microscopic confirmation of the presence of fungal pathogens, and (iii) reisolation of the fungus from the poinsettias. As shown in Fig. 8, the stem-incision inoculation method was the most efficient in producing infection. The host-parasite relationship created by this method resulted in external symptoms on the aerial portions of the host and various amounts of root decay. The soil-probe and soil-drench methods of introducing the pathogen into the root environment resulted in the production of disease symptoms on a small percentage of host plants. The results are based on 10 separate inoculation attempts, each performed at different times but under similar conditions. Twenty poinsettia plants were used each time.

Infection from direct introduction of *Chalaropsis thielavioides* into the host plant through an incision resulted in external symptoms in 78 percent of the plants inoculated while in the vegetative stage. External symptoms were not pronounced and did not develop immediately. The most common symptom was general chlorosis and stunting that became evident only when comparisons were made with the check plants (Fig. 9*A*). Epinastic and curling leaves (Fig. 9*B*) were frequent symptoms that indicated root disorders. A general reduction in the sizes of the root balls of the inoculated plants was evident upon removing the diseased plants from the soil (Fig. 9*C*). In a few cases decaying roots and roots with small lesions were found. The inner surface of the lowest pith chamber of the stem (the inoculation site) was blackened and soft (Fig. 9*D*).

External symptoms were not produced on poinsettias inoculated while in the flowering stage. Occasionally a small area of diseased tissue was found on the inner surface of the inoculated pith chamber of the flowering plants, but these areas failed to become extensive.

Microscopic examinations of scrapings of the inner surfaces of the stems of plants inoculated in the vegetative stage revealed an abundance of chlamydospores, endoconidia, and mycelium of *Chalaropsis* in the decaying host tissue. *Chalaropsis* was cultured consistently from the diseased inner surfaces of the pith chambers.

Quite similar results were obtained when the *Thielaviopsis* isolates were used in stem-incision inoculations. The

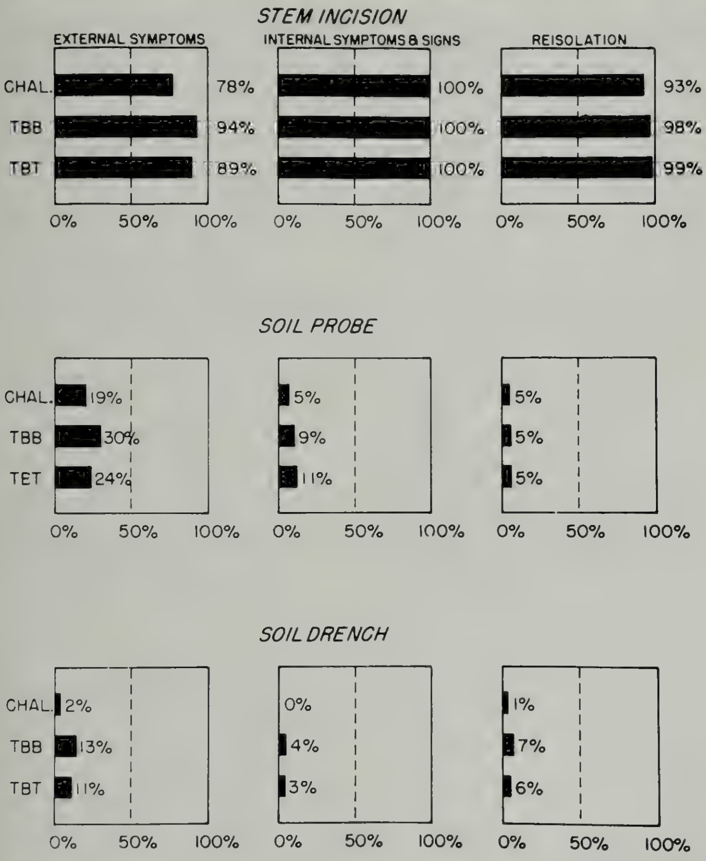

Fig. 8. — A comparison of the disease incidence resulting from three methods of initiating host-pathogen association.

TBB isolate produced external symptoms on 94 percent and the TBT isolate on 89 percent of the plants inoculated in the vegetative stage.

Two groups of symptoms developed on poinsettias that had *Thielaviopsis* introduced into stem incisions while the plants were in the vegetative stage. One group of symptoms appeared soon after the fungus had been implanted, but the other group did not appear until the plants flowered. Soon after the fungus was introduced, many of the plants became stunted and chlorotic (Fig. 10*A*), but many others appeared healthy and exhibited no external symptoms until the time of flowering. The presence or absence of external symptoms appeared to vary with the poinsettia varieties. At approximately the time the upper bracts of the poinsettias began to change color, the lower leaves of the inoculated

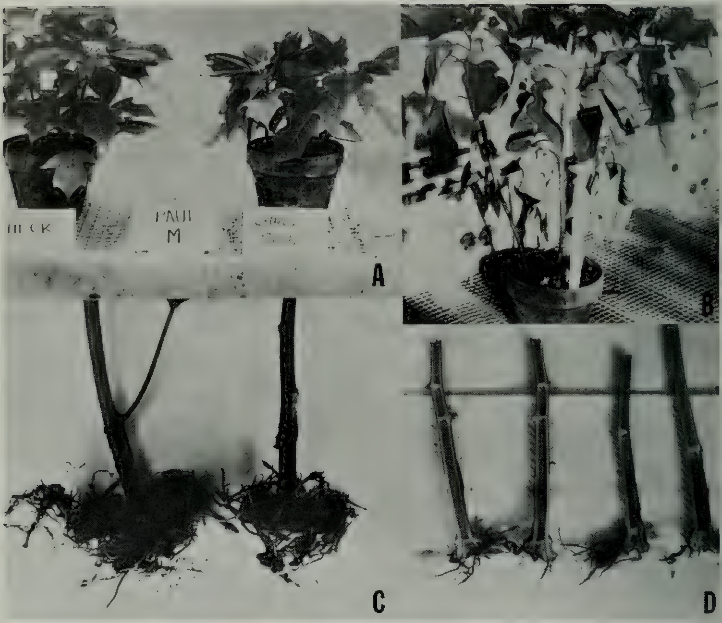

Fig. 9. — Symptoms of Chalaropsis root rot on poinsettias: *A*, stunting of a diseased 120-day-old plant (right) compared to a healthy 120-day-old plant (left); *B*, wilting of leaves from natural infection on a 110-day-old plant; *C*, slightly reduced root ball of diseased plant on right and normal-sized root ball of healthy plant on left; *D*, stem with check incision (left) and stem with incision inoculation (right).

plants began to fall. Leaf fall was progressive, beginning with the lowest leaves and working upward until only the flower bracts were left at the tips of naked stems (Fig. 10*B*). Occasionally wilting preceded leaf fall, but often unwilted leaves were dropped. The root ball was reduced in size. Numerous blackened and decaying roots were conspicuous within the root balls (Fig. 10*C*). Longitudinal sections of the inoculated stems, crowns, and upper root areas of the poinsettias revealed general internal decay throughout the region adjacent to the inoculation slit (Fig. 10*D*). Endoconidia and hyphae were in the stem lesions and on the outer surfaces of the root lesions. *Thielaviopsis* was isolated from the diseased tissues around the inoculation lesions of most plants. However, the symptoms discussed here did not develop on the plants inoculated while in the flowering stage.

The soil-probe method of placing *Chalaropsis* in contact with the poinsettia roots resulted in symptom production on 19 percent of the plants tested. Stunting and chlorosis became evident only after 30–45 days.

Root decay was more extensive on the vegetative poinsettias than on the flowering poinsettias inoculated by the soil-probe method. The aerial portions of flowering poinsettias did not show disease symptoms. Typical symptoms resulting from inoculations by the soil-probe method were extensive root decay and lack of new root development. Reisolation of *Chalaropsis* from the diseased roots was occasionally successful, but interference from soil contaminants usually prevented successful reisolations.

The application of both isolates of *Thielaviopsis* to the roots of poinsettias by the soil-probe method resulted in symptoms slightly different from those produced by *Chalaropsis*. Of the plants that had a soil-probe application of the TBB isolate 30 percent developed external symptoms, and of those receiving an application of the TBT isolate 24 percent developed such symptoms.

No symptoms were produced by *Thielaviopsis* on the aerial parts of poinsettias inoculated while in the flowering stage. Vegetative poinsettias inoculated by applying *Thielaviopsis* to probed soil became slightly chlorotic and stunted within 30–60 days. Infected poinsettias also began to flower 7–10 days earlier than did healthy plants. Lesions began to develop on the crown area of the stem after about 30 days. The outer epidermis and cuticle around the lesion loosened and sloughed off. This was followed by the formation of additional lesions, loosening of the epidermis, and production of callus tissue around the lower stem. Numerous chlamydospores were produced in the lesions. The destruction of roots was extensive. Small areas on the roots or root stubs became discolored and soft. The decay progressed up the root, and in time the entire root became a dark, slimy mass. Endoconidia and hyphae were produced in great abundance on the decaying roots. The entire root balls of most diseased plants decayed and only the lower stem was left in the soil. In such cases the poinsettias usually toppled and died. The amount of disease that developed in a heavily infected greenhouse crop was similar to the re-

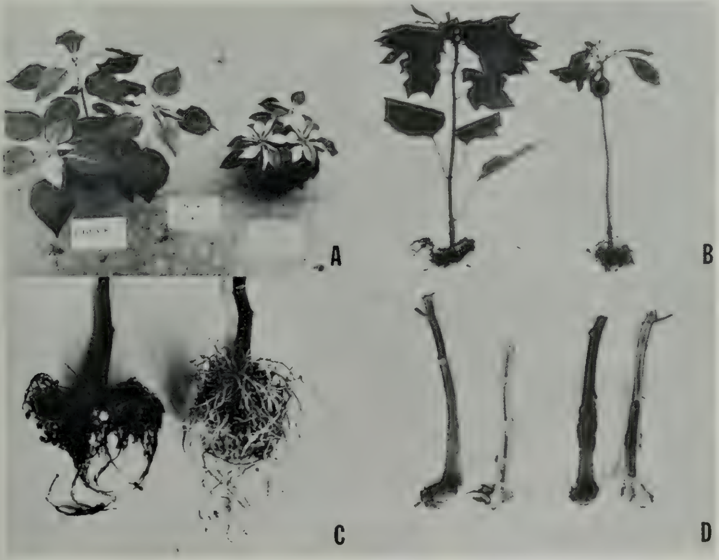

Fig. 10. — Symptoms of Thielaviopsis root rot on poinsettias: *A*, stunted 120-day-old plant (right) and a healthy plant; *B*, leaf drop and stunting of a diseased 95-day-old plant (right) and a healthy 95-day-old plant (left); *C*, root balls of poinsettias — diseased roots on left and healthy ones on right; *D*, stem with check incision (left) and stem with incision inoculation (right).

sults reported by Presley (1947) on the amount of disease in a field situation.

Reisolation from the decaying roots was successful in the few cases in which soil contaminants did not overrun the *Thielaviopsis* colonies.

The introduction of *Chalaropsis* into the poinsettia root environment by the soil-drench method resulted in only slight disease incidence. Symptoms were slight and hardly detectable. Only 2 percent of the inoculated plants appeared slightly chlorotic or stunted or had diseased roots. In a few cases *Chalaropsis* was reisolated, but soil contaminants usually overran the *Chalaropsis*. For every 100 poinsettia plants growing in soils infested with the TBB isolate, 13 developed disease symptoms. Many roots of the diseased plants became decayed and new roots did not develop. The TBT isolate applied in a soil drench produced similar results, but on only 11 percent of the treated plants. As with the previous inoculation method, attempts to reisolate both fungi were usually unsuccessful because of faster growing soil contaminants.

DISCUSSION

The results of pathogenicity tests conducted during this study have shown that *Chalaropsis thielavioides* is a weak pathogen on poinsettias. This fungus is probably not capable of producing its own infection site. However, it is capable of producing disease symptoms on poinsettias after it has entered a plant through wounds. Pathogenicity studies performed during this investigation suggest that poinsettias with intact roots grown under normal conditions will probably not exhibit a high incidence of disease from this fungus even in soil with large concentrations of *Chalaropsis* propagules. The amount of wounding proportionally increases the degree of disease incidence. An abnormal number of broken roots, which might result from rough handling during transplanting or intense watering, may appreciably increase losses from the disease caused by *C. thielavioides*. More extensive root breakage from heavy infestations of insects or from inserting stakes in pots could result in extreme disease losses. Although the death of a few secondary roots from insufficient watering might not directly affect the plant, such a condition could provide entry sites for *Chalaropsis*.

Thielaviopsis is not restricted to entering poinsettias through wounds. Studies show that this fungus can produce an appreciable amount of disease in poinsettias without wounds. However, wounding increases the probability of disease.

Results of some of the cultural studies suggest that environmental conditions may also influence the amount of disease caused by *Chalaropsis* and *Thielaviopsis*. A pH range of about 6.0–8.0 and temperatures from about 20° to 30° C. were most favorable for growth of both fungi in culture. Similar pH and temperature conditions in the soil should result in good development and vigorous growth of the fungi. Since these conditions are not ideal for the growth of poinsettias, the combination of weakened hosts and vigorously growing pathogens should result in a greater disease incidence than would normally be expected.

No work was planned as a part of this investigation to test the effect of variations in soil temperatures on disease development. However, one related experiment did produce the anticipated results. The greenhouse air temperature was increased by 6° C. to induce vigorous flower production. This increase produced a corresponding increase in soil temperature. Using various poinsettia varieties, 150 rooted cuttings were potted in the warmer soils. The soil-probe method was used to inoculate 50 plants with *Chalaropsis* and 50 with *Thielaviopsis;* 50 were injected with distilled water. After 60 days, not a single plant had become diseased. This experiment indicated that increased soil temperatures may reduce disease incidence by inhibiting fungal development. These results support the findings of Blank et al. (1953) in their work on Thielaviopsis root rot of cotton.

Light enhances the production of chlamydospores in *Thielaviopsis* and discourages their formation in *Chalaropsis.* An advanced symptom of *Thielaviopsis* infection is the formation of ground-line lesions in which chlamydospores are found in abundance. Although chlamydospores are occasionally found on diseased roots, their presence there is minor when compared with their presence in the exposed lesions. Colonies of *Thielaviopsis* grown in the light contained multitudes of chlamydospores, while colonies grown in the dark contained far fewer. Since all other factors were equal, the conclusion may be drawn that *Thielaviopsis* chlamydospore production is enhanced by, although not dependent on, the presence of light.

Chalaropsis produced symptoms different from those produced by *Thielaviopsis.* Although advanced Chalaropsis disease symptoms consisted of ground-line lesions and areas of sloughed-off epidermal tissues, chlamydospores were not found in these areas but rather on the internal surfaces of the same areas. In culture, *Chalaropsis* chlamydospores were found abundantly in colonies grown in the dark but seldom in colonies grown in the light. These results prove that chlamydospore production in *Chalaropsis* is favored by darkness.

Results of reisolation attempts prove that the development of *Chalaropsis* and *Thielaviopsis* in poinsettias is restricted to the tissues not containing chlorophyll. Attempts to reisolate the fungi from all parts of diseased poinsettias showed that both fungi grow only in the roots and in the ground-line stem region of the more mature plants. In no instance was either fungus isolated from leaves or upper stems. These results were anticipated after finding no growth of either fungus on the agar made from the aerial structures of poinsettias and poor growth on the agar made from the entire plant. Apparently there is an unknown factor in the chlorophyll-containing tissues that does not exist in the other tissues and that prohibits the growth of *Chalaropsis* and *Thielaviopsis.*

SUMMARY

Poinsettias are subject to root rots that are caused by three fungi, *Thielaviopsis basicola, Rhizoctonia solani,* and *Pythium ultimum,* occurring either individually or in complexes. Infection by these fungi may result in stunting, leaf drop, premature flowering, dwarfed flowers, stem lesions, and occasionally the death of the root. Another fungus, *Chalaropsis thielavioides,* which has not previously been considered a member of the poinsettia root rot complex, was frequently obtained while attempting to isolate *T. basicola.* Instead, *C. thielavioides* has been considered to be a surface saprophyte on roots of many plants, especially carrots. There are few reports of it as a plant pathogen. During an investigation of Thielaviopsis root rot, *C. thielavioides* was repeatedly isolated from the roots of diseased poinsettias exhibiting *Thielaviopsis*-like symptoms. This led to the concept that *Chalaropsis* should be included as part of the root rot complex.

Some of the major characteristics of *Thielaviopsis basicola* and *Chalaropsis thielavioides* are presented for comparison in Table 3.

Two isolates of *Thielaviopsis basicola* and one isolate of *Chalaropsis thielavioides* were selected for comparison in cultural requirements, morphology, and pathogenicity. Nine varieties of poinsettias were used to determine and maintain the pathogenicity of the three fungal isolates. Various media were used to determine the pH requirements and the most suitable culture medium for each of the isolates.

Colony characteristics and morphology were compared for each of the iso-

lates grown in culture. The isolates were grown at six different temperatures to ascertain the optimum temperature for growing each in culture. Media comprising a pH range of 2.7–9.2 were used to determine the optimum pH requirement for each isolate. Cultures of each of the three isolates were grown on several different media both in the light and in the dark to compare the morphological features and growth rates of each isolate under both conditions. Three methods of placing the pathogen in contact with the host were used to determine the pathogenicity of each isolate.

Morphologically, the two fungi compared were similar except for the pro-

Table 3. — Some of the major characteristics of *Thielaviopsis basicola* and *Chalaropsis thielavioides*.

Characteristic	*Thielaviopsis basicola*	*Chalaropsis thielavioides*
Disease produced	Root rot	Root rot, grafting failure
Hosts	Numerous herbaceous plants	Relatively few herbaceous plants, some trees and shrubs
General disease symptoms on poinsettias	Chlorosis, stunting, small root balls, leaf drop, premature flowering	Chlorosis, stunting, small root balls
Advanced disease symptoms on poinsettias	Longitudinal lesions on stem near ground line, girdling of stem, death of host	Internal decay of stem near ground line
Pathogenicity	Strongly pathogenic	Weakly pathogenic
Morphology		
Mycelium	Mostly thin walled and hyaline; some thick walled and dark	Mostly thin walled and hyaline; some thick walled and dark
Endoconidia	Stoutly cylindrical, hyaline, single celled; average measurements: 7.78 x 2.61 μ	Cylindrical, hyaline, single celled; average measurements: 7.6 x 1.7 μ
Chlamydospores	Dark, multispored chains, terminal; average measurements: 19.30 x 5.77 μ; club-shaped chains; unit breaks up into individual spores; no resting period required before germination	Dark, single spores, terminal; average measurements: 7.64 x 7.64 μ; round unit remains intact; resting period required before germination
Environmental requirements		
pH	Optimum range: pH 5.9–6.7	Optimum range: pH 6.7–8.0
Temperature	Optimum range: 24° to 27° C.	Optimum range: 20° to 30° C.
Light	Most growth in the dark	Most growth in the light
Growth rate on V-8 juice agar	Average 5.9 mm in diameter per day	Average 8.0 mm in diameter per day
Mode of entry into host	Capable of producing its own infection site	Requires a wound for entry
Location within diseased poinsettia	Mycelium ramifies host tissue; endoconidia on external and internal surfaces of lower stem and roots	Mycelium ramifies host tissue; endoconidia on external and internal surfaces of lower stem and roots
Site of chlamydospore production on diseased poinsettias	In stem lesions near ground line	On internal surfaces of lower pith chambers of stem
Anticipated disease incidence on poinsettias in heavily infested soils	With no root damage: 12 percent With some root damage: 27 percent	With no root damage: 2 percent With some root damage: 19 percent

duction of chlamydospores. Chlamydospores of *Thielaviopsis* were produced in club-shaped chains composed of three to seven spores. *Chalaropsis* chlamydospores were spherical and were produced individually.

Light enhanced the formation of chlamydospores in *Thielaviopsis* and inhibited their formation in *Chalaropsis*. An advanced symptom of *Thielaviopsis* infection was the formation of ground-line lesions in which chlamydospores were found in abundance. Culture colonies of *Thielaviopsis* grown in the light contained multitudes of chlamydospores, while colonies grown in the dark contained far fewer.

Advanced disease symptoms of *Chalaropsis* infection were characteristically ground-line lesions and areas of sloughed-off epidermal tissues. Chlamydospores were not found in these areas but rather on the internal walls of the stem pith chambers near the ground line. In culture, chlamydospores were found abundantly in *Chalaropsis* colonies grown in the dark but seldom in colonies grown in the light. These results confirmed that chlamydospore development in *Chalaropsis* is inhibited by the presence of light.

The results of isolation attempts proved that the development of these isolates of *Chalaropsis thielavioides* and *Thielaviopsis basicola* on poinsettias is restricted to nonchlorophyllous tissues. Both fungi were frequently isolated from the roots and ground-line stem tissues of diseased poinsettias but never from the upper stems, leaves, or flowers.

Both isolates of *Thielaviopsis* grew best in culture on media with a pH range of 6.0–7.0. The *Chalaropsis* isolate grew best on agar media with a pH range of 7.0–8.0. The greatest growth of *Chalaropsis* occurred at 30° C. The optimum temperature for growth of both isolates of *Thielaviopsis* was 25° C.

The results of the pathogenicity tests showed *Chalaropsis thielavioides* to be a weak pathogen. This fungus was probably not capable of producing its own infection site. It was capable of producing disease symptoms on poinsettias similar to the symptoms produced by *Thielaviopsis* after it had entered the host plant through wounds.

Thielaviopsis was not restricted to wounds for entry. Pathogenicity tests showed that this fungus could produce appreciable amounts of disease on unwounded host plants, although wounding did increase disease incidence.

Similarities between *Chalaropsis thielavioides* and *Thielaviopsis basicola* were numerous. Morphology and colony characteristics indicated a possible relationship between these two genera. Growth factors, dimensions of comparable structures, similar vegetative and reproductive structures, and the production of similar disease symptoms on poinsettias were some of the characteristics that these two fungi had in common. Some specific factors such as the location of chlamydospore production and pathogenicity on poinsettias were points in which the two were different. *T. basicola* is important for its role as a component in the root rot complex of numerous plants, including poinsettias. *C. thielavioides* is not of major importance as a plant pathogen. The work presented here proves that *Chalaropsis* is a weak pathogen on poinsettias.

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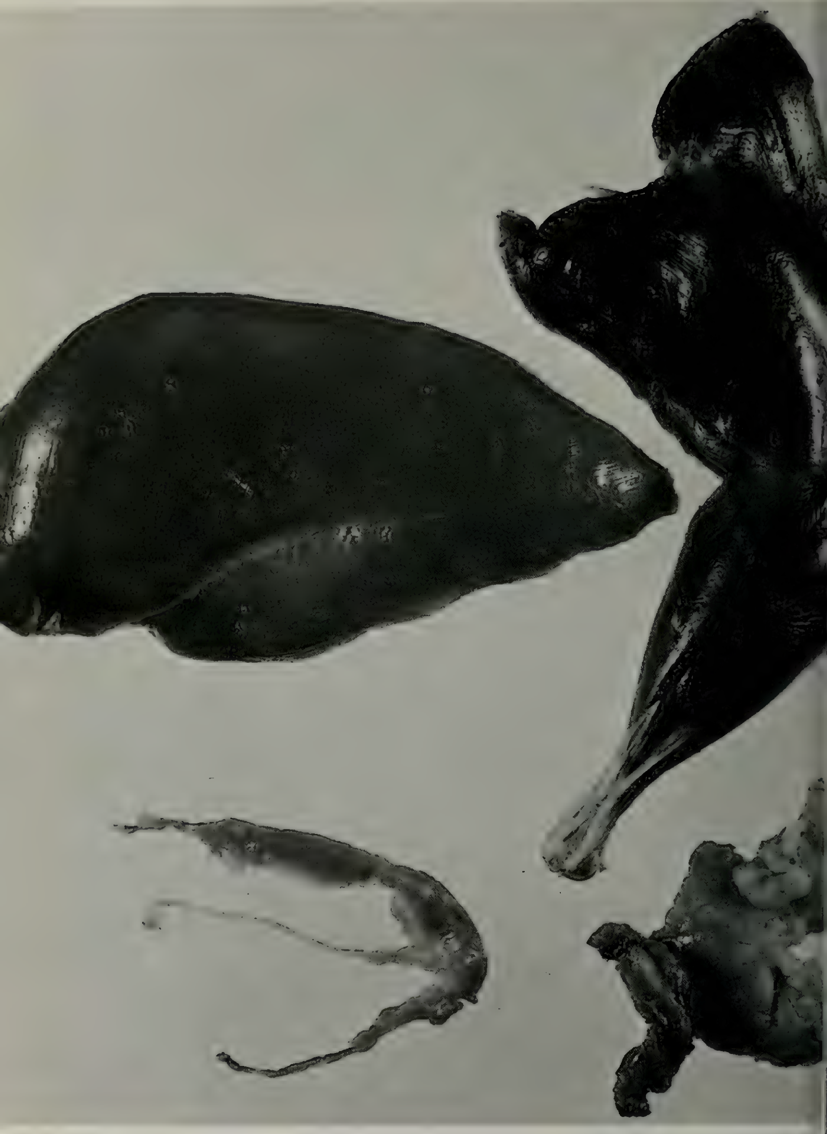

Frontispiece.—The sternal muscles, leg, fat strip, and visceral fat as they appear after being excised from a hen pl

Dynamics of Condition Parameters and Organ Measurements in Pheasants

William L. Anderson

ENVIRONMENTAL FACTORS are recognized as the primary forces dictating the distribution, abundance, and physical condition of pheasants (*Phasianus colchicus*) and all other game species. These forces, whether beneficial or detrimental, manifest themselves within the physiological mechanisms carrying on the life processes of individuals constituting animal populations. Thus, it might be said that the physiological status of an animal is the expression of all of the environmental factors acting on the animal. This study elucidates changes in selected physiological parameters of wild pheasants in Illinois in relation to stresses that occur during the life cycle of this game bird.

The study was initiated in 1966 to provide base lines for evaluating the physiology of pheasants in fair and poor range in Illinois (Anderson 1969). However, it soon became evident that the findings provide information applicable not only to the practical management of pheasants, but to the basic knowledge about birds in general. Equally important, the findings provide background information for other studies, particularly those concerned with the effects of organic pesticides, toxic minerals, and other environmental pollutants on birds. The actions of toxins in birds appear to be strongly influenced by the physiological status, especially the stage of energy balance, of the specimens being studied. Thus, whether test specimens are in positive or negative energy balance is minimal background information for any study of interrelationships between toxic substances and birds.

This investigation was inspired by Kirkpatrick's (1944) study of "Body Weights and Organ Measurements in Relation to Age and Season in Ring-necked Pheasants" and by Hanson's (1962*a*) study of *The Dynamics of Condition Factors in Canada Geese and Their Relation to Seasonal Stresses.*

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Dr. Robert P. Breitenbach, Professor of Biological Sciences, Department of Zoology, University of Missouri, Columbia, reviewed the manuscript and made many valuable suggestions. Dr. Horace W. Norton, Professor of Statistical Design and Analysis, Department of Animal Sciences, University of Illinois, Urbana, offered advice on statistical aspects of the study.

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METHODS

The research for this study involved collecting 363 pheasants (274 hens and 89 cocks) from wild populations in east-central Illinois, weighing them, and dissecting them to obtain weights or measurements of muscular tissues, fat deposits, and internal organs. The pheasants were collected during designated periods in the life cycle, from 1966 through 1969 (Table 1) in Ford and Livingston counties and in portions of Champaign and McLean counties adjacent to Ford and Livingston counties. These counties, located in the heart of Illinois' better pheasant range (Labisky 1969:7), are under intensive cultivation; about 90 percent of the total land area is cropped annually for corn, soybeans, oats, and tame hay.

The periods of the life cycle in which pheasants were collected were somewhat arbitrarily designated as growth, fall, winter, prebreeding, breeding (and laying for hens), incubating (hens only), and molting. The molting period for adults coincides in time with the growth period for juveniles.

The methods used in collecting pheasants were nightlighting (Labisky 1968*a*), shooting (through the head) with a compressed-air rifle, and salvaging birds killed or injured by mowing machines (Table 1). In addition, a few birds, particularly during the breeding period, were taken with a shotgun or were found dead along roads. Except for hens collected during the incubating period, which were picked up after they had been hit by hay mowers, most of the pheasants were sacrificed during the first 3 hours after sunrise. Pheasants collected by nightlighting were placed in an inverted position and decapitated to allow the blood to flow from the carcass. Similarly, birds shot with guns or injured by mowing machines were decapitated immediately after being taken in hand, usually 15–30 seconds after they had been hit. After being sacrificed, the birds were placed individually in polyethylene bags and refrigerated (2° C.) or frozen (−15° C.) until they could be dissected.

For the purposes of this study, all pheasants less than approximately 13 months of age—i.e., pheasants that had not entered into their first postnuptial molt—were considered *juveniles*, and all older birds were considered *adults*. This classification simplifies the presentation and discussion of the data as the birds progress through the seven designated periods of the life cycle. *Juveniles* were distinguished from *adults* by measuring the depth of the bursa during the fall and winter periods and by measuring the diameter and length of the proximal primary flight feathers (Wishart 1969) during the prebreeding, breeding, and incubating periods. During the latter three periods, *juveniles* were approximately 1 year old and *adults* were approximately 2 years old, 3 years old, etc. Juveniles collected during the growth and fall periods were further aged, to the nearest week, by examining the advancement of the molt of the primary feathers (Labisky 1968*b*:465).

The tissues and organs that were excised and weighed were the muscles of the right half of the sternum (*pectoralis thoracica, supracoracoideus*-ventral head, and *coracobrachialis*, nomenclature by Hudson & Lanzillotti 1964:13–15) and the entire right leg (i.e., all muscles and bones of the thigh and shank); the fat strip and visceral fat (Breitenbach, Nagra, & Meyer 1963:25); the liver, heart, spleen, pancreas, gizzard, and reproductive organs (left—i.e., the developed—ovary and left—developed—oviduct or both testes); both kidneys, both lungs, both parathyroids, both

Table 1.—Dates and principal methods of collecting pheasants in east-central Illinois, 1966 through 1969.

Age and Period	*Hens*					*Cocks*	*Collection Methods*
	1966	1967	1968	1969	All Years	All Years [a]	
Juveniles							
Growth	7/26– 9/12[b]	7/21– 8/10[b]	7/24– 8/5[b]	. . .	7/21– 9/12[b]	7/11– 9/13[e]	Shooting
Fall	10/26–11/2[c]	10/24–10/26[c]	10/15–10/26[c]	10/22–10/23[c]	10/15– 11/2[c]	10/14–11/2[f]	Nightlighting
Winter	2/23	1/13	2/15– 2/16	1/11– 1/14	1/11– 2/23	2/15– 2/16	Nightlighting
Prebreeding	. . .	. . .	4/3 – 4/9	4/9 – 4/11	4/3 – 4/11	4/2 – 4/18	Nightlighting, shooting
Breeding	. . .	4/25– 6/2	4/29– 5/28	4/28– 5/22	4/25– 6/2	4/22– 6/9	Shooting, salvaging dead birds along roads
Incubating	. . .	6/5 – 7/6	6/8 – 6/18	6/9 – 6/16	6/5 – 7/6	. . .	Salvaging birds killed by mowers
Adults							
Molting	7/25– 8/17[d]	7/18– 8/30[d]	7/16– 8/5[d]	7/23– 8/2[d]	7/16– 8/30[d]	7/11– 8/17[g]	Shooting
Fall	10/5 –10/26	10/24–10/26	10/14–10/26	10/22–10/23	10/5 –10/26	10/10–10/26	Nightlighting
Winter	1/27– 2/23	1/13	2/15– 2/16	1/11– 1/14	1/11– 2/23	. . .	Nightlighting
Prebreeding	. . .	. . .	4/3 – 4/9	4/8 – 4/11	4/3 – 4/11	. . .	Nightlighting, shooting
Breeding	. . .	4/28– 5/19	4/22– 5/29	4/28– 5/22	4/22– 5/29	. . .	Shooting, salvaging dead birds along roads
Incubating	. . .	6/16– 6/20	6/8 – 6/24	6/11– 6/17	6/8 – 6/24	. . .	Salvaging birds killed by mowers

[a] 1966, 1967, and 1968

[b] Mean ages were 7.0±1.3, 6.8±0.6, 6.8±0.4, and 6.9±0.4 weeks in 1966, 1967, 1968, and all years, respectively

[c] Mean ages were 17.5±0.8, 17.5±0.7, 19.0±0.4, 17.9±0.7, and 18.0±0.3 weeks in 1966, 1967, 1968, 1969, and all years, respectively

[d] Had molted an average of 4.0±0.5, 3.6±0.8, 3.8±0.2, 3.4±0.3, and 3.7±0.2 primary feathers in 1966, 1967, 1968, 1969, and all years, respectively

[e] Mean age was 6.6±0.4 weeks

[f] Mean age was 18.3±0.6 weeks

[g] Had molted an average of 4.9±0.3 primary feathers.

thyroids, both adrenals, and both thymuses; and the bursa. The lengths of the intestine, ceca, and colon were measured, using the procedure described by Leopold (1953); if one cecum was longer than the other, the average of the two was recorded.

After being freed of extraneous material, the tissues and organs were rolled on paper towels to remove excess moisture and blood and were then weighed. The heart and liver were cut open to remove clots of blood, and the gall bladder was removed from the liver. The contents, but not the lining, were removed from the gizzard. This organ was separated from the proventriculus by severing the latter at its posterior constriction; thus, a small portion of the proventriculus was retained with the gizzard.

The sternal muscles, leg, fat strip, and visceral fat, as they appear after being prepared for weighing, are illustrated in the Frontispiece. The weights of sternal muscles and of legs were doubled when the data were analyzed.

All weight data presented in this paper represent the wet (fresh) weights of the tissues and organs. I recognize that the percentage of water present can vary and, hence, can affect the wet weight of the tissues and organs.

Data were also obtained for (i) the number of ruptured follicles in the ovaries of breeding hens (Meyer, Kabat, & Buss 1947), (ii) the stage of incubation of eggs in nests associated with incubating hens (Labisky & Opsahl 1958), (iii) the advancement of the molt of the primary feathers of growing juveniles and of molting adults, and (iv) the length of the wing (Anderson & Stewart 1969:256).

Complete data were not obtained for all birds in all periods in all years of the study. Notable in this respect was the lack of data for adrenals, parathyroids, and thyroids for 1966 and for legs, intestines, ceca, and colons in 1969. Cocks were collected only sporadically from 1966 through 1968 and not at all in 1969. Endocrine glands were excised from the pheasants collected in 1966. However, because my dissecting techniques were not perfected at that time and because I removed only the right adrenal, parathyroid, and thyroid and then doubled their weights, I chose to discard the data obtained for these glands in 1966.

When the data were assembled and examined, it was evident that the number of pheasants of a designated sex, age, period, and year was usually minimal (Table 2). This problem of small samples became more critical when I learned that the pheasants collected during the prebreeding, breeding, and incubating periods in 1967, 1968, and 1969 could be identified as juveniles or adults. Formerly, I had placed all pheasants collected during these periods in the adult category. Determining the ages of these birds became possible when Wishart (1969) described a technique for separating juvenile pheasants from adults by measuring their proximal primary feathers. I had saved and kept in cold storage (−15° C.) both wings from each pheasant collected in 1967, 1968, and 1969. Thus, it became necessary to split my samples for prebreeding hens, breeding hens, and incubating hens. It was also necessary to omit pheasants taken during the prebreeding, breeding, and incubating periods of 1966—their wings had not been saved. Because of the small sample sizes and, to a lesser extent, because of the volume of data otherwise involved, I chose to present my findings without regard to the year of collection. The only exception is in the presentation of the findings for body weight.

FINDINGS

In this investigation, body weight—i.e., the weight of the entire bird—and the weights of muscular tissues and of fat deposits were used as indices of physical condition. Data on weights or measurements of visceral organs and of endocrine glands are presented and discussed primarily as they relate to changes in the physical condition and seasonal activities of pheasants.

Condition Parameters

SEX-AGE DIFFERENCES.—The mean weights of the entire bird, sternal muscles, legs, fat strip, and visceral fat from pheasants collected during this study are summarized in Tables 2–4. When differences between the sex-age groups were tested statistically, it was apparent that many significant ($P<0.05$) differences existed between the mean weights for hens and cocks and between the mean weights for juveniles and adults (Tables 5 and 6).

It is common knowledge that body weight, and corresponding masses of flesh, are smaller among hens than among cocks. However, when expressed as percentages of body weight,

Table 2.—Mean body weights (entire bird) and standard errors, in grams, of pheasants collected in east-central Illinois, 1966 through 1969. Sample sizes are in parentheses.

Age and Period	*Hens*					*Cocks*
	1966	1967	1968	1969	All Years	All Years
Juveniles						
Growth	365±99 (5)	323±35 (6)	310±42 (5)	. . .	332±34 (16)	350±30 (17)
Fall	841±17 (9)	874±26 (6)	858±20 (8)	822±13 (10)	845±9 (33)	1,176±17 (12)
Winter	852±46 (3)	875±19 (6)	865±15 (10)	861±26 (10)	864±11 (29)	1,170±22 (5)
Prebreeding	. . .	. . .	893±29 (4)	994±28 (10)	965±24 (14)	1,314±20 (13)
Breeding	. . .	1,063±32 (7)	1,041±25 (5)	1,031±17 (18)	1,040±13 (30)	1,239±24 (17)
Incubating	. . .	818±10 (8)	890±35 (8)	856±71 (3)	854±19 (19)	. . .
Adults						
Molting	787±18 (7)	818±12 (7)	818±16 (10)	808±24 (10)	808±9 (34)	1,131±19 (17)
Fall	901±44 (6)	901±18 (5)	924±18 (7)	911±27 (10)	910±14 (28)	1,304±18 (8)
Winter	946±34 (4)	943±31 (8)	927±17 (6)	1,013±36 (10)	965±17 (28)	1,386±22[a] (12)
Prebreeding	. . .	. . .	1,132±36 (6)	1,142±35 (10)	1,138±25 (16)	. . .
Breeding	. . .	1,119±26 (4)	1,113±30 (6)	1,107±22 (7)	1,112±14 (17)	. . .
Incubating	. . .	900±21 (3)	865±33 (4)	877±66 (3)	879±22 (10)	. . .

[a] From cocks captured January 15–February 14, 1963 (S. L. Etter, Illinois Natural History Survey, Urbana, unpublished data).

the mean weights of sternal muscles during the breeding and molting periods, and of legs during the prebreeding and breeding periods, were also smaller among hens than among cocks. It is pertinent that the only times when the mean relative weights of sternal muscles were smaller among hens than among cocks occurred during the breeding and molting periods. The smaller mean relative weights of the sternal muscles in hens during these periods presumably were a reflection of protein catabolism induced by the high-protein requirements of egg production. The mean weights of fat deposits, both absolute and relative to body weight, were similar between the sexes during the fall and winter periods, but differed significantly during

Table 3.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of sternal muscles and legs from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*[a]		*Sternal Muscles*		*Legs*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	63.3±7.9 (18.5±0.6)	64.3±6.2 (18.1±0.3)	66.9±8.1 (19.6±0.7)	70.7±6.8 (19.9±0.3)
Fall	33	12	213.2±3.3 (25.2±0.2)	284.7±4.9 (24.2±0.4)	187.5±3.3[b] (21.9±0.3)	263.2±5.6 (22.4±0.2)
Winter	29	5	233.3±3.4 (27.0±0.3)	316.0±7.8 (27.0±0.3)	177.6±3.0[c] (20.5±0.2)	243.0±6.5 (20.8±0.3)
Prebreeding	14	13	240.8±6.1 (25.0±0.3)	322.4±6.5 (24.5±0.3)	179.8±7.7[d] (20.1±0.3)	283.8±6.0 (21.6±0.3)
Breeding	30	17	232.1±4.3 (22.3±0.2)	299.6±6.4 (24.2±0.2)	189.4±5.2[e] (18.0±0.3)	275.4±6.8[l] (22.2±0.2)
Incubating	18	..	215.4±5.7 (25.1±0.3)	...	177.9±4.6[f] (20.8±0.4)	...
Adults						
Molting	34	17	196.6±2.9 (24.3±0.2)	286.5±5.4 (25.4±0.5)	185.2±3.1[g] (22.9±0.2)	262.9±5.6 (23.2±0.2)
Fall	28	8	229.7±4.2 (25.3±0.3)	321.1±7.6 (24.6±0.5)	191.5±3.7[h] (21.1±0.2)	287.0±5.5 (22.0±0.3)
Winter	28	..	252.2±4.5 (26.2±0.3)	...	187.5±3.7[h] (20.0±0.2)	...
Prebreeding	16	..	262.9±6.0 (23.2±0.5)	...	204.0±9.0[i] (18.0±0.5)	...
Breeding	17	..	246.2±4.0 (22.2±0.3)	...	188.2±3.8[j] (16.9±0.3)	...
Incubating	10	..	216.7±6.2 (24.6±0.3)	...	183.7±8.3[k] (20.8±0.7)	...

[a] As the following footnotes indicate, sample size sometimes varied from the number shown in this column.

[b] n=23. [c] n=19. [d] n=4. [e] n=12. [f] n=15. [g] n=24. [h] n=18. [i] n=6. [j] n=10. [k] n=7. [l] n=16.

Table 4.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of fat strips and visceral fat from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Fat Strip*		*Visceral Fat*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	0.04±0.01 (0.01±0.00)	0.04±0.01 (0.01±0.00)	0.16±0.03 (0.05±0.01)	0.20±0.04 (0.05±0.01)
Fall	33	12	0.33±0.05) (0.04±0.01)	0.31±0.08 (0.03±0.01)	1.6 ±0.3 (0.18±0.03)	1.15±0.33 (0.10±0.03)
Winter	29	5	0.78±0.09 (0.09±0.01)	0.56±0.17 (0.05±0.01)	4.4 ±0.8 (0.50±0.09)	2.38±0.92 (0.20±0.07)
Prebreeding	14	13	2.9 ±0.3 (0.30±0.03)	1.00±0.20 (0.08±0.01)	17.4 ±2.4 (1.78±0.22)	4.94±1.19 (0.37±0.09)
Breeding	30	16	2.2 ±0.2 (0.21±0.02)	0.50±0.14 (0.04±0.01)	14.7 ±1.3 (1.40±0.12)	1.93±0.59 (0.15±0.05)
Incubating	19	..	1.4 ±0.2 (0.16±0.02)	...	8.1 ±1.0 (0.94±0.11)	...
Adults						
Molting	34	17	0.22±0.03 (0.03±0.00)	0.16±0.03 (0.01±0.00)	0.82±0.13 (0.10±0.02)	0.51±0.08 (0.04±0.01)
Fall	28	8	0.74±0.16 (0.08±0.02)	0.56±0.14 (0.04±0.01)	3.6 ±1.1 (0.38±0.11)	2.11±0.54 (0.16±0.04)
Winter	28	..	1.92±0.25 (0.19±0.02)	...	10.6 ±2.8[a] (1.05±0.14)	...
Prebreeding	16	..	5.4 ±0.7 (0.47±0.05)	...	32.5 ±4.7 (2.80±0.36)	...
Breeding	17	..	3.6 ±0.3 (0.33±0.02)	...	23.4 ±1.8 (2.08±0.14)	...
Incubating	10	..	1.5 ±0.4 (0.16±0.04)	...	9.2 ±2.0 (1.02±0.21)	...

[a] n=27.

the prebreeding and breeding periods, when hens were much fatter than cocks.

When pheasants collected during the same periods were compared, the mean weights of the entire bird and of the sternal muscles were lower for juveniles than for adults (Table 6). However, the mean relative weights of sternal muscles did not differ significantly between the two age groups. For legs, the mean relative weights were greater for juvenile hens than for adult hens during the fall, prebreeding, and breeding periods. The mean weights of the fat strip and visceral fat were approximately half as great for juvenile hens as for adult hens during all periods except the incubating period. These findings suggest that, from the standpoint of energy reserves, juvenile hens differ greatly from adult hens dur-

Table 5.—Differences, hens compared with cocks, in mean weights of the entire bird, muscular tissues, fat deposits, and internal organs of pheasants collected in east-central Illinois, 1966 through 1969 (Tables 2−4, 12−16, and 18−20). Plus signs indicate that mean weights were larger, and minus signs smaller, for hens than for cocks and that the differences were statistically significant ($P < 0.05$) as indicated by analysis of variance. The signs in parentheses represent differences in mean weights when expressed as percentages of body weight.

Tissue or Organ	*Juveniles*					*Adults*	
	Growth[a]	Fall	Winter	Prebreeding	Breeding	Molting	Fall
Entire bird	. .	−	−	−	−	−	−
Sternal muscles	. .	− (+)	−	−	− (−)	− (−)	−
Legs	. .	−	−	− (−)	− (−)	−	− (−)
Fat strip	. .	. .	. .	+ (+)	+ (+)	(+)	. .
Visceral fat	. .	. .	. .	+ (+)	+ (+)	(+)	. .
Liver	. .	−	−	−	+ (+)	−	−
Kidneys	. .	−	−	−	(+)	−	−
Heart	. .	− (−)	− (−)	− (−)	− (−)	− (−)	− (−)
Lungs	. .	− (−)	− (−)	− (−)	− (−)	− (−)	− (−)
Pancreas	. .	− (+)	(+)	(+)	. .	−	−
Spleen	. .	−	. .	(+)	. .	− (+)	−
Gizzard	. .	− (+)	− (+)	(+)	(+)	(+)	− (+)
Intestine	. .	−	. .	. .	+	. .	−
Cecum	. .	−	−	. .	. .	. .	−
Colon	. .	−	−	. .	+	. .	. .
Parathyroids	. .	. .	. .	. .	(+)	(+)	. .
Thyroids	. .	−	. .	−	(+)	(+)	−
Adrenals	. .	−	−	− (−)	. .	− (+)	−
Thymuses	. .	−	. .	(+)	. .	. .	. .

[a] No significant differences occurred between juvenile hens and cocks during the growth period.

Table 6.—Differences, juveniles compared with adults, in mean weights of the entire bird, muscular tissues, fat deposits, and internal organs of pheasants collected in east-central Illinois, 1966 through 1969 (Tables 2 – 4 and 12 – 20). Plus signs indicate that mean weights were larger, and minus signs smaller, for juveniles than for adults and that the differences were statistically significant ($P < 0.05$) as indicated by analysis of variance. The signs in parentheses represent differences in mean weights when expressed as percentages of body weight.

Tissue or Organ	*Hens*					*Cocks*
	Fall	Winter	Prebreeding	Breeding	Incubating	Fall
Entire bird	−	−	−	−	. .	−
Sternal muscles	−	−	− (+)	−	. .	−
Legs	(+)	−	(+)	(+)	. .	−
Fat strip	− (−)	− (−)	− (−)	− (−)	. .	. .
Visceral fat	−	− (−)	− (−)	− (−)	. .	. .
Liver	. .	. .	−	(+)	. .	. .
Kidneys	. .	−	. .	. .	. .	. .
Heart	−	(+)	(+)	. .	. .	−
Lungs	. .	. .	. .	. .	. .	. .
Pancreas	. .	. .	(+)	(+)	. .	. .
Spleen	. .	. .	. .	+ (+)	. .	. .
Gizzard	(+)	(+)	. .	(+)	. .	(+)
Intestine	. .	. .	. .	. .	. .	. .
Cecum	+	. .	. .	. .	. .	. .
Colon	. .	. .	. .	. .	. .	. .
Ovary or testes	− (−)	− (−)	. .	. .	. .	−
Oviduct	− (−)	− (−)	− (−)	. .	. .	. .
Parathyroids	− (−)	. .	−	+ (+)	. .	−
Thyroids	. .	. .	−	(+)	. .	. .
Adrenals	−	. .	. .	. .	. .	. .
Thymuses	+ (+)	+ (+)	. .	+ (+)	+ (+)	+ (+)

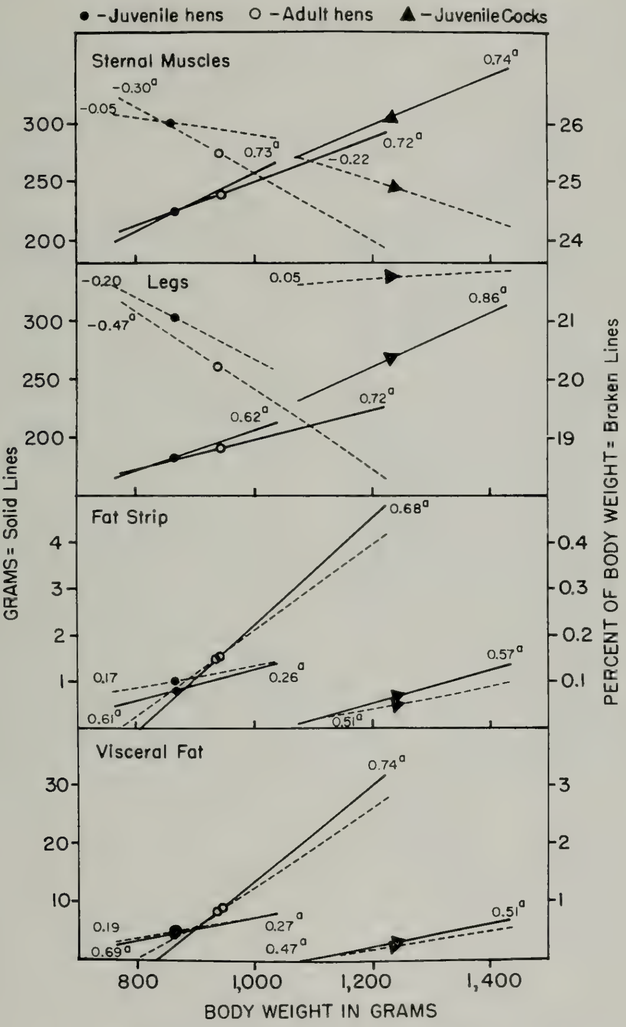

Fig. 1.—Relationships, as determined by linear correlations, between body weight and the weights of sternal muscles, legs, fat strips, and visceral fat of pheasants in east-central Illinois. The correlation coefficients (*r*) are at the ends of the lines, and where the letter *a* follows the coefficient, the correlation was significant ($P < 0.05$). The pheasants were collected during the fall, winter, prebreeding, and, for hens, incubating periods, 1966 through 1968. The degrees of freedom are 57 for juvenile hens, 46 for adult hens, and 26 for juvenile cocks.

ing the fall, winter, prebreeding, and breeding periods. The potential importance of these differences is expanded upon in the discussion section.

BODY WEIGHT VERSUS MUSCULAR TISSUES AND FAT DEPOSITS.—It is an axiom that the weight of the entire bird depends on the weights of the component parts of the body. Therefore, in pheasants the weights of muscular tissues and of fat deposits can be expected to correlate with body weight. Linear correlations indicated that, indeed, the weights of sternal muscles, legs, fat strips, and visceral fat were positively correlated with body weight (Fig. 1). However, when expressed on a relative basis, the weights of sternal muscles and of legs tended to be inversely related to body weight. The weights of the fat strip and of visceral fat, regardless of how they were expressed, were positively correlated with body weight. It appeared that seasonal variations in the body weights of pheasants were determined primarily by variations in the amounts of fat in the birds. Kabat, Meyer, Flakas, & Hine (1956:30–31), who studied captive pheasants, came to similar conclusions. This does not preclude the fact that heavy (large) birds can be relatively fat free and that light (small) birds can contain appreciable amounts of fat.

Because body weight and structural dimensions vary considerably among pheasants, a condition index derived from some combination of these two parameters might be more closely related to the weights of muscular tissues and fat deposits than is body weight alone. Bailey (1968) developed a condition index for the cottontail rabbit (*Sylvilagus floridanus*) using the relationship between body weight and total length, and Harris (1970:750) used body weight divided by the product of bill length times keel length for evaluating the physical condition of the blue-winged teal (*Anas discors*).

Accordingly, I calculated a condition index for pheasants by dividing the cube root of body weight in grams by wing length in decimeters. Amadon (1943:171–172) recommended converting body weight to its cube root to reduce the variability of this measurement to a level comparable to the vari-

Table 7.—Correlation coefficients (*r*) for relationships between body weight and the weights of the sternal muscles, legs, fat strip, and visceral fat and between a condition index and the weights of these body parts of pheasants collected in east-central Illinois, 1966 through 1969. The condition index was calculated by dividing the cube root of body weight in grams by wing length in decimeters. The correlation coefficients in parentheses are for the weights of the tissues when expressed as percentages of body weight. The pheasants were collected during the fall, winter, prebreeding, and, for hens, incubating periods.

Tissue	*Juvenile Hens*		*Adult Hens*		*Juvenile Cocks*	
	Body Weight	Condition Index	Body Weight	Condition Index	Body Weight	Condition Index
	df=57		df=46		df=26	
Sternal muscles	0.727[a] (–0.047)	0.313[a] (–0.009)	0.724[a] (–0.297)[a]	0.425[a] (–0.370)[a]	0.737[a] (–0.220)	0.375[a] (–0.337)
Legs	0.619[a] (–0.203)	0.045 (–0.367)[a]	0.723[a] (–0.469)[a]	0.481[a] (–0.406)[a]	0.858[a] (0.052)	0.709[a] (0.300)
Fat strip	0.258 (0.168)	0.469[a] (0.433)[a]	0.683[a] (0.610)[a]	0.627[a] (0.592)[a]	0.566[a] (0.507)[a]	0.405[a] (0.387)[a]
Visceral fat	0.266[a] (0.187)	0.431[a] (0.399)[a]	0.744[a] (0.686)[a]	0.666[a] (0.647)[a]	0.512[a] (0.473)[a]	0.372 (0.364)

[a] The correlation was significant ($P < 0.05$)

ability of wing length. Linear correlations indicated that this condition index was statistically related to the weights of the sternal muscles, legs, fat strip, and visceral fat (except visceral fat of juvenile cocks) among all sex-age groups of pheasants included in these analyses (Table 7). However, correlation coefficients for body weight alone were, for the most part, comparable to those for the condition index. These findings suggested that body weight alone was as reliable as this particular condition index for evaluating the physical condition of pheasants.

CONDITION PARAMETERS DURING STARVATION.—Because of the labile character of the body, condition parameters of starved pheasants should be especially helpful in interpreting "normal" shifts in metabolic reserves. Data for starved pheasants were obtained during another study (Anderson 1969) in which 10 juvenile hens were experimentally starved to death during the fall and 7 were starved to death during the winter (Table 8). The pheasants were held in outdoor cages for these experiments. During both periods, the birds lost an average of slightly more than 50 percent of their initial body weight. Estimates made by making comparisons with hens not starved indicated that the experimental birds lost approximately 75 percent of the weight of their sternal muscles, 55 percent of the weight of their legs, and more than 90 percent of the weights of their fat deposits. Decreases in the combined weights of sternal muscles and legs accounted for an estimated 62 percent of the loss of body weight during the fall experiment and a 53-percent loss during the winter experiment. The hens starved during the fall survived an average of 8.8 ± 0.4 days and lost body weight at an average rate of 49.6 ± 2.4 grams per day, whereas those starved

Table 8.—Mean weights and standard errors, in grams, of the entire bird, muscular tissues, fat deposits, and livers from juvenile hen pheasants experimentally starved to death during November 1966 and during January 1967. The values in parentheses are the means of the weights when expressed as percentages of body weight. The November group achieved a mean survival time of 8.8±0.4 days, and the mean survival time of the January group was 11.6±0.5 days. The hens were captured from wild populations in east-central Illinois.

Tissue or Organ	*November 1–13, 1966 Group* (n=10)[a]		*January 12–26, 1967 Group* (n=7)	
	Weight	Percent of Initial Weight	Weight	Percent of Initial Weight
Entire bird	418 ± 12	49[b]	441 ± 16	46[c]
Sternal muscles	52.9 ± 2.8 (12.6 ± 0.5)	25[d] (50)	49.5 ± 3.6 (11.2 ± 0.5)	21[d] (41)
Legs	81.4 ± 3.7 (19.4 ± 0.4)	43[d] (89)	85.9 ± 3.7 (19.5 ± 0.4)	48[d] (95)
Fat strip	0.02± 0.00 (0.01± 0.00)	6[d] (25)	0.06± 0.01 (0.01± 0.00)	8[d] (11)
Visceral fat	0.02± 0.01 (0.01± 0.00)	1[d] (6)	0.14± 0.03 (0.04± 0.01)	3[d] (8)
Liver	6.9 ± 0.3 (1.65± 0.05)	46[d] (92)	8.3 ± 0.3 (1.90± 0.11)	52[d] (103)

[a] These birds were aged according to the advancement of the molt of the primary flight feathers (Labisky 1968*b*:465). The 10th primary averaged 109±12 mm in length, and the mean age of this group was 18.7±0.6 weeks.

[b] The initial weight of the hens averaged 847±14 grams, which was close to the norm for juvenile hens in fall (Table 2)

[c] The initial weight of the hens averaged 963±27 grams, 11 percent greater than juvenile hens normally weigh in winter (Table 2)

[d] Estimated by making comparisons with hens not starved (Tables 3, 4, and 12)

during the winter survived an average of 11.6 ± 0.5 days and lost body weight at an average rate of 45.5 ± 1.9 grams per day.

Tester & Olson (1959:306–307) reported that wild pheasants held in outdoor pens at Madelia, Minn., and experimentally starved during the winter survived an average of 11–12 days and lost an average of 52–53 percent of their body weight—findings that concur with mine. Kabat et al. (1956:25) held birds in cages in an unheated building at Poynette, Wis., and reported that in two separate experiments wild hens died after an average of 16 and 19 days without food during the winter months; the birds lost an average of 28.0 and 30.4 grams of body weight per day (Kabat et al. 1956: 11,25). Errington (1939:28) reported that captive pheasants of both sexes lost an average of 45 percent of their initial weights before dying of starvation; this experiment was conducted during the winter at Lansing, Iowa. Hanson (1962*a*:10) found that free-living Canada geese (*Branta canadensis interior*) lost 43–46 percent of their initial weight when starved during the fall.

Several workers have pointed out the importance of body weight or status of metabolic reserves in withstanding starvation (Benedict & Lee 1937:92; Kendeigh 1945:218; Kabat et al. 1956: 14; and Tester & Olson 1959:306). It is noteworthy that in my experiment the juvenile hens starved during the winter survived an average of 2.8 days (32 percent) longer than did the juvenile hens starved during the fall and that, at the beginning of the experiment, the mean body weight was 14 percent greater for the former than for the latter (Table 8).

Seasonal Changes in Body Weight.—Seasonal changes in the body weights of pheasants have received considerable attention (Kirkpatrick 1944:178; Kabat, Thompson, & Kozlik 1950:25; Kabat et al. 1956:29; Breitenbach & Meyer 1959:1018; Breitenbach et al. 1963: 26; and Edwards, Mikolaj, & Leite 1964). Typically, pheasants attain their heaviest annual weights at the onset of the breeding period and decline in weight thereafter—i.e., through the breeding and incubating periods and into the molting period. However, Kirkpatrick (1944:178), in his study of captive pheasants, found that juvenile birds attained their greatest weight in early winter (December).

The body weights of pheasants collected in east-central Illinois exhibited seasonal changes typical of the classic pattern (Fig. 2). The mean weights of juvenile hens, relative to their mean weight during the winter, were 112 percent during the prebreeding period, 120 percent during the breeding period, 99 percent during the incubating period, and 94 percent during the molting period. During the same periods, the mean weights of adult hens, compared with the mean weights of juvenile hens in the winter, were 132, 129, 102, and 94 percent, respectively. The mean weights of juvenile cocks, relative to the weights of wintering juvenile cocks, were 112, 106, and 97 percent during the prebreeding, breeding, and molting periods, respectively.

My selection of the winter juvenile as the standard for comparison parallels Hanson's (1962*a*:17) decision to use the wintering bird as the basic type for Canada geese. Winter is the period when juvenile pheasants have completed growth but, unlike adults, are not "excessively" fat; pheasants are not undergoing dramatic physiological processes such as egg laying, incubating, or molting; and, in Illinois, food is abundant and usually available. In essence, I consider body weight and other physiological parameters of the winter juvenile to be representative of pheasants in minimum, or near minimum, good condition.

In this study, adult hens were heaviest during the prebreeding period, whereas juvenile hens did not attain their greatest mean weight until the

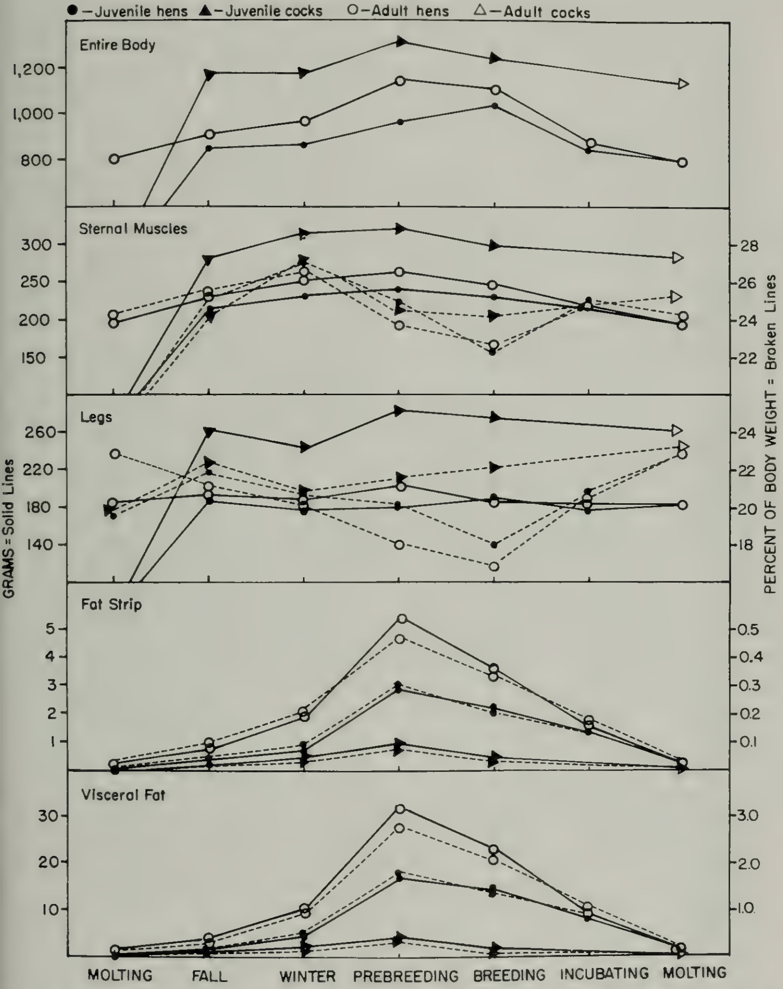

Fig. 2.—Seasonal changes in mean weights of the entire body, sternal muscles, legs, fat strip, and visceral fat of pheasants in east-central Illinois, 1966 through 1969. Statistics for the mean values are presented in Tables 2—4.

breeding period—about 1 month later. In reality, both juvenile hens and adult hens were probably heaviest the day they began to lay eggs. By counting the ruptured follicles in the ovary of each hen and allowing 1.3 days for each egg laid (Labisky & Jackson 1966:384), it was estimated that, in east-central Illinois during 1967–1969, the average juvenile hen (n=30) and the average adult hen (n=17) began laying on April 29 ± 1.8 days and April 20 ± 1.6 days, respectively. The difference between these dates was statistically significant ($P<0.05$).

Much of the increase in the mean body weights from the winter to the prebreeding period was attributable to increased deposits of fat. The increase averaged 101 grams among juvenile hens, 173 grams among adult hens, and 144 grams among juvenile cocks. During the prebreeding period, the fat strip and visceral fat were, on the average, at least twice as large as they were during the winter period (Fig. 2). The mean weights of sternal muscles and legs, except the legs of cocks, exhibited only modest increases between the two periods (Fig. 2), as did the mean weights of most of the internal organs (Tables 12–17). Sternal muscles, legs, and internal organs (excluding the intestine, ceca, and colon) collectively contributed 18 percent (18 grams), 27 percent (46 grams), and 42 percent (61 grams) to the winter-prebreeding increase in the mean body weights of juvenile hens, adult hens, and juvenile cocks, respectively.

Unlike adult hens and juvenile cocks, juvenile hens increased in mean body weight by 75 grams (8 percent) from the prebreeding period to the breeding period; yet the mean weights of their sternal muscles and fat deposits exhibited concurrent decreases (Fig. 2). In this instance, most of the increase in body weight was caused by increases in the weights of the legs and internal organs; the combined weights of the ovary and oviduct accounted for 61 percent (46 grams) of the increase.

After attaining a peak in mean body weight during the prebreeding period, adult hens lost weight during the breeding and incubating periods, and the weight loss continued into the molting period (Fig. 2). Similarly, juvenile cocks decreased in mean body weight from the prebreeding period through the breeding period to the molting period. The mean body weights of juvenile hens also decreased during the incubating period and into the molting period after attaining their peak during the breeding period. I assumed that juvenile hens and adult hens were not significantly different in mean body weight and in the weights of muscular tissues and of fat deposits by the time the birds entered the molting period. Data obtained during the previous (incubating) period, when hens could be identified as juveniles or adults, indicated that this assumption was justifiable (Tables 2–4).

Although nearly all portions of the body that were weighed or measured decreased in mean weight or mean length between the prebreeding period and the molting period, much of the decline in the mean body weights was due to the reduction of fat deposits (Fig. 2). The mean weights of the fat strip and visceral fat, respectively, declined 92 and 95 percent in juvenile hens, 96 and 97 percent in adult hens, and 84 and 90 percent in juvenile cocks. Decreases in the weights of muscular tissues, especially sternal muscles, also contributed importantly to the prebreeding-to-molting loss of body weight; sternal muscles and legs together accounted for 25 percent of the decrease in the mean body weight of juvenile hens, 26 percent of the decrease in adult hens, and 31 percent of the decrease in juvenile cocks.

The mean body weight of adult hens and that of adult cocks increased 13 and 15 percent, respectively, between the molting and fall periods (Table 2). During the latter period, adult hens weighed an average of 910 grams, 105 percent of the average weight of the basic type (winter juvenile). Much of the molting-to-fall increase in mean body weight was caused by increases in the mass of muscular tissue, particularly the sternal muscles. Sternal muscles and legs contributed an average of 38 percent (39 grams) to the increase in the mean body weight of adult hens and 34 percent (59 grams) to the increase in the mean body weight of adult cocks. Fat deposits also contributed to the increase in the mean body weight of adults between the molting and fall periods.

By late October, when 18 weeks of age, juvenile pheasants had attained mean body weights only slightly lower than those of wintering juveniles (Fig. 2).

SEASONAL CHANGES IN MUSCULAR TISSUES.—Changes in the mean weights of sternal muscles and legs exhibited patterns similar to those of mean body weight (Fig. 2). The mean weights of sternal muscles increased slightly (3 percent for juvenile hens, 4 percent for adult hens, and 2 percent for juvenile cocks) from winter to the prebreeding period. The mean weights of the legs of juvenile hens and of adult hens also increased slightly (1 and 9 percent, respectively) between these periods, whereas the mean weights of the legs of juvenile cocks increased appreciably (17 percent). Sternal muscles and legs, except the legs of juvenile hens, were heavier, on the average, during the prebreeding period than during any other period in the life cycle. However, when expressed as percentages of body weight, the mean weights of sternal muscles and of legs, except the legs of juvenile cocks, exhibited pronounced decreases between the winter period and the prebreeding period. Obviously, concurrent increases in body weight, caused primarily by the enlargement of fat deposits, were proportionally greater than those of muscular tissues, particularly among hens.

The mean weights of sternal muscles decreased during the breeding period and, in hens, during the incubating period, and eventually descended to their annual low during the molting period (Fig. 2). From the prebreeding to molting periods the mean weights of the sternal muscles of juvenile hens decreased an average of 18 percent, those of adult hens 25 percent, and those of juvenile cocks 11 percent. When compared with those of the basic type (wintering juveniles), the mean weights of the sternal muscles of molting birds were 84 percent of "normal" for adult hens and 91 percent of "normal" for adult cocks. The mean weights of the legs of adult hens and juvenile cocks also decreased (9 and 7 percent, respectively) from the prebreeding period to the molting period, whereas the mean weights of the legs of juvenile hens increased slightly (3 percent). However, the mean weights of the legs of adult hens and adult cocks during the molting period were greater (104 and 108 percent as great) than the mean weights of the legs of wintering juveniles.

The increases in the mean weights of the legs of juvenile hens and adult hens (4 and 1 percent, respectively) between the incubating and molting periods (Fig. 2) were presumably a use-disuse phenomenon; the legs of hens would obviously be much more active during the molting period than during the incubating period. Hanson (1962*a*:20) has demonstrated that the leg muscles of Canada geese become enlarged during the nonflying stages of the molt.

When expressed relative to body weight, weights of sternal muscles and legs, except the legs of juvenile cocks, decreased, on the average, from the prebreeding period to the breeding period. However, among hens the decline in the mean weights of muscular tissues relative to body weight did not extend into the incubating period. In fact, notable increases (11–23 percent) in the mean relative weights of the sternal muscles and legs of both juvenile hens and adult hens occurred between the breeding and incubating periods. Apparently, muscular tissue was shrinking at a faster rate than were fat deposits during the breeding period, while the reverse was true when the hens were incubating.

The sternal muscles and legs of both adult hens and adult cocks increased in mean weight from the molting period to the fall period (Table 3). The mean weights of sternal muscles excised from fall-collected adult hens and adult cocks were 98 and 102 percent, respectively, as great as those of the sternal muscles of wintering juveniles. Similarly, the mean weights of the legs of adult hens and of adult cocks were 108 and 118 percent as great, respectively, as the mean weights of the legs of juvenile hens and of juvenile cocks in winter. It appeared that molting-to-fall gains in the mean weights of muscular tissue were of sufficient magnitude to restore fully the protein reserves lost during the nesting season.

The mean weights of the sternal muscles of juvenile hens and juvenile cocks collected during the fall were only 91 and 90 percent, respectively, as great as those of wintering juveniles (Fig. 2). However, the mean weights of the legs of juvenile hens and juvenile cocks were greater (106 and 108 percent as great, respectively) during the fall than during the winter.

Seasonal Changes in Fat Deposits.—Seasonal changes in mean weights, both absolute and relative to body weight, of the fat strip and of visceral fat were essentially the same (Fig. 2). These changes held true for both hens and cocks. The mean weights of fat deposits increased greatly, threefold among juvenile hens and adult hens and twofold among juvenile cocks, from winter to the prebreeding period, when fat deposits were at their heaviest annual weight. Breitenbach & Meyer (1959:1019) reported similar findings in captive pheasants.

The fat deposits decreased in mean weight from the prebreeding period to the breeding period and, for hens, to the incubating period. The mean weights of the fat strip and visceral fat of adult hens and adult cocks were at their annual lows during the molting period, being only about 25 percent as great as those of wintering juveniles. The fat deposits of adult hens and adult cocks increased in mean weight between the molting and fall periods and, by the latter period, they were similar in weight to the fat deposits of wintering juveniles.

The mean weights of the fat strip and of visceral fat from juvenile hens and juvenile cocks during the fall ranged from 36 to 55 percent of the mean weights of these fat deposits in wintering juveniles (Fig. 2).

Relationships Between Condition Parameters and Breeding, Incubating, and Molting Activities.—It has been demonstrated that body weight and the weights of muscular tissues and fat deposits undergo important changes during the pheasant's annual cycle. But how do these condition parameters respond to specific stresses which the birds must endure to survive and reproduce? To answer this question in part, data for pheasants actively engaged in breeding, incubating, or molting were analyzed by regressions. Body weight and the weights of muscular tissues and fat deposits were designated the dependent variables, and the number of eggs laid, days of incubating, or number of primary feathers molted, the independent variable. The dates that pheasants were collected were also included and were considered the second independent variable. Thus, the initial analysis evolved into multiple regressions. To increase the sample sizes for breeding hens and for incubating hens, the data for juveniles and adults were combined.

Analysis of variance indicated that—except for the body weight, sternal muscles, and legs of incubating hens—significant regressions existed between the condition parameters and the independent variables (Tables 9–11). The fat strip and visceral fat, both in actual weight and when expressed as percentages of body weight, exhibited significant regressions with the independent variables in every possible instance. The sternal muscles and legs of breeding hens and of molting hens and molting cocks, when expressed in actual weight or percentages of body weight, or both, exhibited significant relationships with the independent variables.

Correlation coefficients indicated that linear correlations between the independent variables—eggs laid and collection date—for breeding hens, and between the independent variables—primary feathers molted and collection

Table 9.—Results of multiple regressions involving condition parameters (Y), eggs laid (X_1), and collection date (X_2) for hen pheasants, juveniles and adults combined, taken during the breeding period, 1967 through 1969, in east-central Illinois. The values in parentheses are for the condition parameters when expressed as percentages of body weight. The correlation coefficient (r) for eggs laid and collection date was 0.69 with 45 degrees of freedom ($P < 0.05$).

Condition Parameter (Y)	*Degrees of Freedom*	*Analysis of Variance* (*F*)	*t Value*[a]	
			For Eggs Laid (X_1)	For Collection Date (X_2)
Body weight	2 & 44	6.32[b]	1.46	3.35[b]
Sternal muscles	2 & 44	8.74[b] (2.68)	0.77	3.49[b]
Legs	2 & 19	8.94[b] (1.67)	2.69[b]	4.18[b]
Fat strip	2 & 44	13.61[b] (12.27)[b]	1.39 (1.25)	4.59[b] (4.32)[b]
Visceral fat	2 & 44	10.86[b] (9.68)[b]	1.54 (1.39)	4.24[b] (3.97)[b]

[a] These *t* values equal the unstandardized regression coefficient divided by the standard error of the unstandardized regression coefficient

[b] These *F* values and *t* values were statistically significant ($P<0.05$).

Table 10.—Results of multiple regressions involving condition parameters (Y), days of incubating (X_1), and collection date (X_2) for hen pheasants, juveniles and adults combined, taken during the incubation period, 1967 through 1969, in east-central Illinois. The values in parentheses are for the condition parameters when expressed as percentages of body weight. The correlation coefficient (r) for days of incubating and collection date was 0.26 with 26 degrees of freedom ($P > 0.05$).

Condition Parameter (Y)	*Degrees of Freedom*	*Analysis of Variance* (*F*)	*t Value*[a]	
			For Days of Incubating (X_1)	For Collection Date (X_2)
Body weight	2 & 25	1.25	...	...
Sternal muscles	2 & 25	0.91 (0.12)	...	...
Legs	2 & 19	0.17 (2.38)	...	...
Fat strip	2 & 25	3.64[b] (3.77)[b]	0.22 (0.27)	2.54[b] (2.56)[b]
Visceral fat	2 & 25	3.68[b] (3.79)[b]	0.67 (0.80)	2.36[b] (2.33)[b]

[a] These *t* values equal the unstandardized regression coefficient divided by the standard error of the unstandardized regression coefficient.

[b] These *F* values and *t* values were statistically significant ($P<0.05$)

date—for molting hens and molting cocks were significant ($r = 0.69$, 0.96, and 0.98, respectively). However, the linear correlation between the independent variables—days of incubating and collection date—for incubating hens was not significant ($r = 0.26$).

To determine whether the first independent variable or the second, or both, contributed significantly to the multiple regressions, appropriate t values were calculated for the independent variables (Tables 9–11). Surprisingly, these tests indicated that the second independent variable—collection date—contributed more to the regressions for breeding hens and incubating hens than did the first independent variable—number of eggs laid and days of incubating, respectively. Among molting pheasants, the only t values that achieved significance were those for the first independent variable—primary feathers molted—in the

Table 11.—Results of multiple regressions involving condition parameters (Y), primary feathers molted (X_1), and collection date (X_2) for pheasants taken during the molting and fall periods, 1966 through 1969, in east-central Illinois. The values in parentheses are for the condition parameters when expressed as percentages of body weight. The correlation coefficient (r) for primaries molted and collection date was 0.96 with 60 degrees of freedom ($P<0.05$) for adult hens and 0.98 with 23 degrees of freedom ($P<0.05$) for adult cocks.

Condition Parameter (Y)	*Degrees of Freedom*	*Analysis of Variance* (F)	*t Value* [a]	
			For Primaries Molted (X_1)	For Collection Date (X_2)
Adult hens				
Body weight	2 & 59	20.07 [b]	1.56	0.27
Sternal muscles	2 & 59	24.37 [b] (3.44) [b]	1.61 (0.50)	0.40 (0.26)
Legs	2 & 39	0.79 (18.34) [b]	. . . (1.63)	. . . (0.24)
Fat strip	2 & 59	10.34 [b] (10.07) [b]	2.92 [b] (2.94) [b]	1.80 (1.84)
Visceral fat	2 & 59	7.46 [b] (7.51) [b]	2.51 [b] (2.54) [b]	1.56 (1.60)
Adult cocks				
Body weight	2 & 22	11.49 [b]	0.37	1.25
Sternal muscles	2 & 22	5.87 [b] (0.66)	0.85	1.45
Legs	2 & 22	2.41 (4.52) [b]	. . . (0.13)	. . . (0.43)
Fat strip	2 & 22	6.10 [b] (5.28) [b]	0.08 (0.17)	0.73 (0.76)
Visceral fat	2 & 22	7.18 [b] (6.59) [b]	0.03 (0.01)	0.67 (0.67)

[a] These t values equal the unstandardized regression coefficient divided by the standard error of the unstandardized regression coefficient.

[b] These F values and t values were statistically significant ($P<0.05$).

regressions in which the fat strip and visceral fat of adult hens were the dependent variables. Superficially, this lack of significance seems peculiar because some of the multiple regressions for molting hens and for molting cocks had large *F* values (Table 11). However, according to Dr. Horace W. Norton, Professor of Statistical Design and Analysis, Department of Animal Science, University of Illinois, Urbana (personal communication), this phenomenon is characteristic of multiple regressions in which the independent variables are strongly correlated with each other. It appears that, for the most part, the two independent variables—number of primary feathers molted and collection date—are about equal in their contributions to the multiple regressions for molting pheasants. Kabat et al. (1950:11), who studied captive pheasants, concluded that the relationship between the progression of the molt and changes in body weight was of a secondary nature.

The reason that collection date emerged as a dominant variable in dictating the changes in condition parameters of breeding, incubating, and molting pheasants is difficult to pinpoint. However, many factors—e.g., photoperiod, temperature, precipitation, humidity, plant phenology, and the behavior and physiology of birds—can be associated with date of collection as well as with each other. In the regressions presented above, collection date probably served as a quantified expression of the many factors that influenced the condition parameters of pheasants during the breeding, incubating, and molting periods.

Computations were also made to determine whether curvilinear (second-degree polynomial) regressions existed between the condition parameters and collection dates for pheasants during the breeding, incubating, and molting periods. Almost all sets of data that exhibited significant ($P<0.05$) linear regressions also exhibited significant curvilinear regressions. However, when subjected to a statistical test (Steel & Torrie 1960: 339–340), none of the curvilinear regressions deviated significantly from linearity.

Linear regressions between the condition parameters and collection dates for breeding hens, breeding cocks, incubating hens, and molting hens and molting cocks are plotted in Fig. 3–6. In general, as the date of collection advanced, the condition parameters for breeding and for incubating pheasants decreased in value and those for molting pheasants increased in value. Among breeding pheasants and molting pheasants, the changes in condition parameters in relation to collection dates exhibited similar patterns for the two sexes. The same was true of condition parameters for juvenile hens and adult hens during the breeding period and the incubating period.

The regressions indicated that the body weights of hens (juveniles and adults combined) decreased an average of 2.94 grams (0.26 percent of estimated initial weight) per day during the breeding (laying) period (Fig. 3). Similarly, sternal muscles and legs decreased an average of 1.05 and 0.65 grams (0.40 and 0.32 percent of estimated initial weights), respectively, per day during the breeding period. The fat strip and visceral fat of breeding hens decreased, according to the regressions, an average of 0.07 and 0.41 gram (1.63 and 1.50 percent of estimated initial weights) per day, respectively. Changes in the weights of sternal muscles, legs, fat strip, and visceral fat alone accounted for 74 percent (2.18 grams) of the daily decrease in the body weight of hens during the breeding period.

Condition parameters for cock pheasants also tended to decrease in value during the breeding period (Fig. 4). Linear regressions suggested that the sternal muscles decreased an estimated 0.87 gram (0.28 percent of estimated initial weight) per day and the fat strip an estimated 0.02 gram (2.20 percent of estimated initial weight) per day. Linear regressions between the collection date and body weight, weight of legs, and weight of visceral

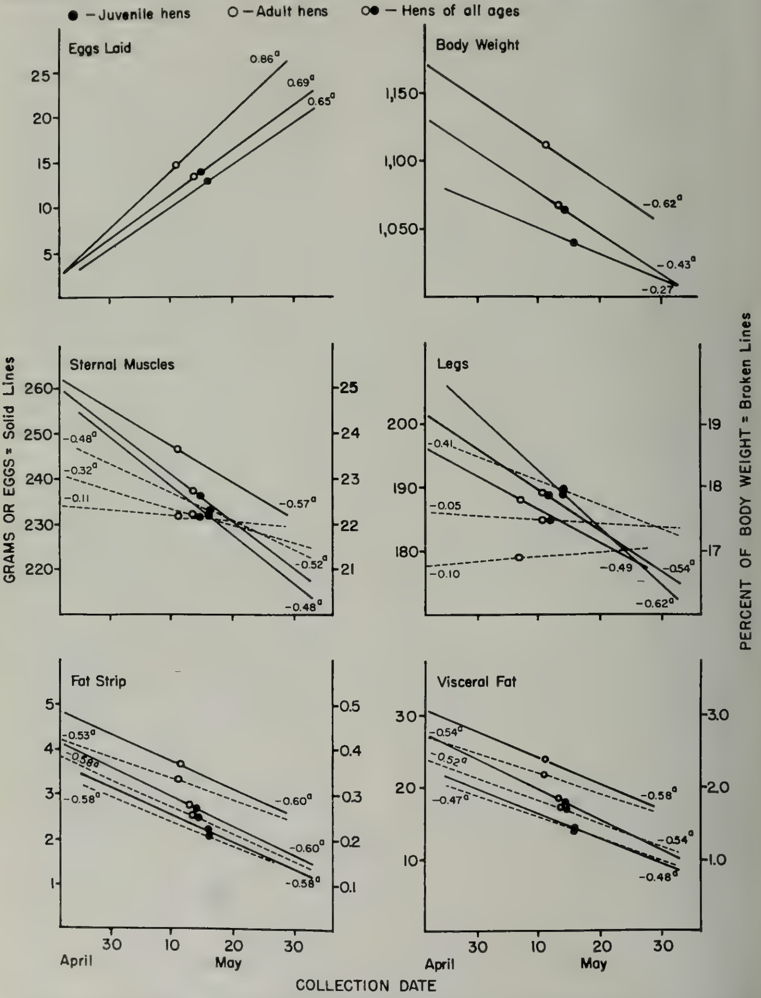

Fig. 3.—Linear regressions involving condition parameters and eggs laid (Y) and collection date (X) for hen pheasants taken during the breeding period, 1967 through 1969, in east-central Illinois. The correlation coefficients (*r*) are at the ends of the lines, and where the letter *a* follows the coefficient, the regression was significant ($P < 0.05$). The degrees of freedom are 28 for juvenile hens, 15 for adult hens, and 45 for hens of all ages (for legs, 10 for juveniles, 8 for adults, and 20 for hens of all ages).

fat of breeding cocks were not statistically significant.

During the incubating period, the fat strip and visceral fat of hens decreased, on the average, 0.07 and 0.37 gram (3.10 and 2.97 percent of estimated ini-

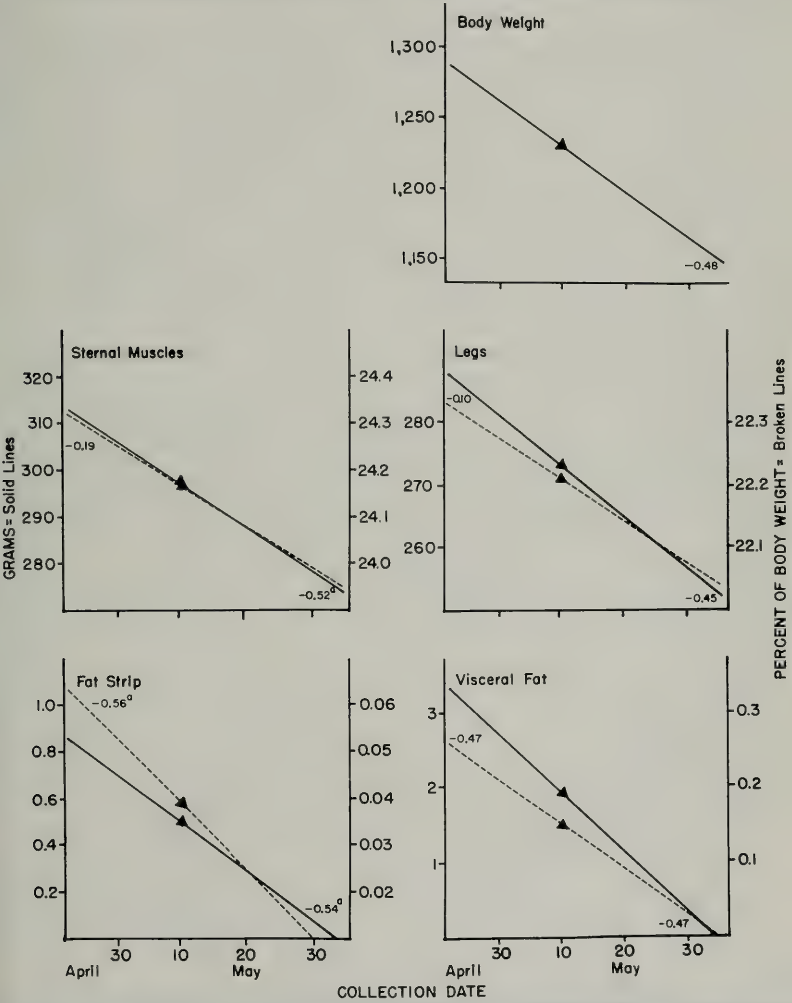

Fig. 4.—Linear regressions involving condition parameters (Y) and collection date (X) for juvenile cock pheasants taken during the breeding period, 1966 through 1968, in east-central Illinois. The correlation coefficients (*r*) are at the ends of the lines, and where the letter *a* follows the coefficient, the regression was significant ($P < 0.05$). The degrees of freedom are 13.

tial weights) per day, respectively (Fig. 5). The implied decreases in body weight, weight of sternal muscles, and weight of legs of incubating hens were not statistically significant.

During the molting and fall periods,

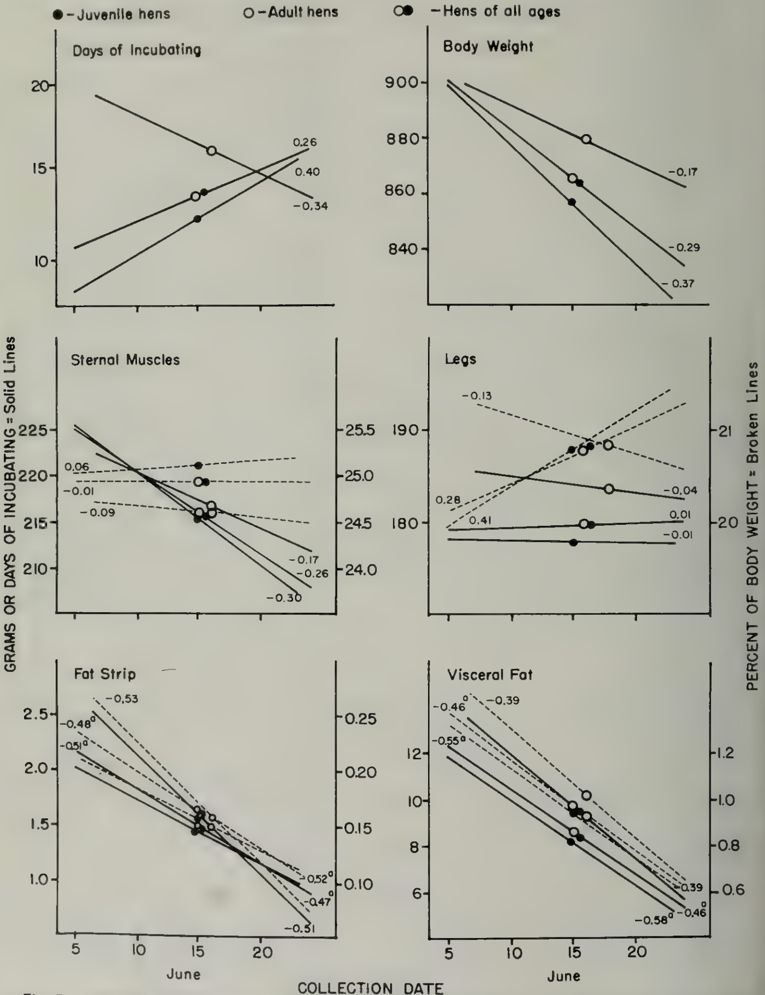

Fig. 5.—Linear regressions involving condition parameters and days of incubating (Y) and collection date (X) for hen pheasants taken during the incubating period, 1967 through 1969, in east-central Illinois. The correlation coefficients (*r*) are at the ends of the lines, and where the letter *a* follows the coefficient, the regression was significant ($P < 0.05$). The degrees of freedom are 16 for juvenile hens, 8 for adult hens, and 26 for hens of all ages (for legs, 13 for juveniles, 5 for adults, and 20 for hens of all ages).

when the pheasants were developing new plumage, the body weight of adult hens increased an average of 1.15 grams (0.15 percent of estimated initial weight) per day, and the body weight of adult cocks increased an average of

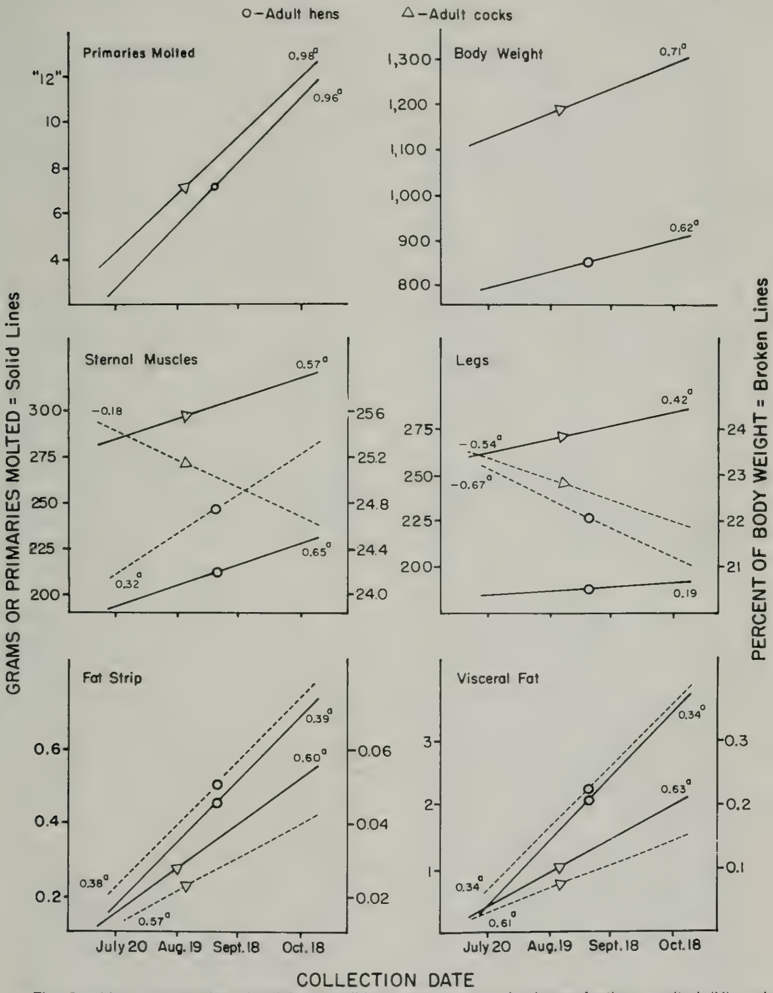

Fig. 6.—Linear regressions involving condition parameters and primary feathers molted (Y) and collection date (X) for adult hen pheasants and adult cock pheasants taken during the molting and fall periods, 1966 through 1969, in east-central Illinois. The correlation coefficients (*r*) are at the ends of the lines, and where the letter *a* follows the coefficient, the regression was significant ($P < 0.05$). The degrees of freedom are 60 for adult hens and 23 for adult cocks (for legs, 40 for hens and 23 for cocks).

1.85 grams (0.17 percent of estimated initial weight) per day (Fig. 6). Except for the legs of hens, the muscular tissues and fat deposits of both hens and cocks exhibited similar, and statistically significant, increases when the birds were molting. However, when expressed relative to body weight, the legs of adult hens and the sternal muscles and legs of adult cocks decreased in weight as the collection date progressed. Contrary to these trends, the relative weights of the sternal muscles of adult hens increased with the passage of time; i.e., the sternal muscles of adult hens gained weight at faster rates than did their entire bodies.

The rates at which body tissues increased in weight during the molting period were much slower than the rates at which they lost weight during the breeding and incubating periods (Fig. 3–6).

Internal Organs

SEX-AGE DIFFERENCES.—When expressed on a relative basis, the mean weights of the heart and lungs were smaller for hens than for cocks (Table 5). These differences were statistically significant during all periods except the growth period. However, the mean relative weights of the pancreas and gizzard were larger for hens than for cocks during most periods. Mitchell, Card, & Hamilton (1931:108) have reported similar sex-associated differences for the heart and gizzard in domestic chickens (*Gallus gallus*), as has Hanson (1962*b*:65, 68) for the gizzard and pancreas in Canada geese. The mean relative weights of the liver, kidneys, parathyroids, and thyroids, and the mean actual lengths of the intestine and colon, were greater for juvenile hen pheasants than for juvenile cocks during the breeding period (Table 5).

When juvenile pheasants were compared with adults, the mean weights of reproductive organs were lower for the former than they were for the latter during the fall and winter periods (Table 6). However, juveniles had, on the average, heavier gizzards and thymuses than adults had during most of the annual cycle. Also, the mean weights of the livers, pancreases, spleens, gizzards, parathyroids, and thyroids were greater for juvenile hens than they were for adult hens during the breeding period, apparently because adult hens were exceedingly heavy (fat) during this period. As might be expected, young, growing pheasants had, on the average, proportionately heavier organs than had older birds (Tables 12–20); the heart, lungs, and reproductive organs were the only exceptions.

SEASONAL CHANGES IN INTERNAL ORGANS.—Seasonal changes in the mean weights and measurements of internal organs of pheasants in east-central Illinois are documented in Tables 12–20. Except for the gizzards and thymuses of juvenile cocks, all of the organs in all of the sex-age groups increased in mean weight from winter to the prebreeding or breeding period. The mean weights of the organs of hens were, for the most part, greater during the prebreeding or breeding period than during any other period in the life cycle. Secondary increases in the mean weights of internal organs were evident during the fall period. In fact, several organs of juvenile cocks, especially those associated with the digestive tract, were at peak mean weights during this period. However, the heart, lungs, and adrenals of cocks were noticeably heavier, on the average, during the prebreeding period than during any other time in the annual cycle.

The increased mean weight of the livers of hen pheasants during the breeding period (Table 12) was presumably a response to estrogen secretion, which undoubtedly was at maximum levels in these birds. Estrogen promotes the accumulation of fat and protein in the liver (Common, Bolton, & Rutledge 1948:265). The only time in the life cycle that mean liver weights were larger for hens than they were for

Table 12.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of the liver and kidneys from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Liver*		*Kidneys*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	8.0 ±0.8 (2.45±0.11)	8.6 ±0.7 (2.50±0.07)	2.5 ±0.2 (0.78±0.03)	2.7 ±0.2 (0.82±0.04)
Fall	33	12	15.1 ±0.6 (1.80±0.08)	21.8 ±0.8 (1.85±0.06)	4.7 ±0.2 (0.56±0.02)	5.9 ±0.3 (0.50±0.03)
Winter	29	5	16.0 ±0.6 (1.85±0.08)	19.3 ±1.1 (1.65±0.09)	3.6 ±0.2[a] (0.41±0.02)	4.5 ±0.3 (0.39±0.02)
Prebreeding	14	13	18.5 ±0.9 (1.91±0.08)	22.2 ±0.9 (1.69±0.07)	4.4 ±0.2 (0.46±0.02)	5.3 ±0.2 (0.41±0.02)
Breeding	30	17	23.7 ±0.7 (2.29±0.06)	18.6 ±0.7 (1.50±0.05)	5.7 ±0.2[b] (0.55±0.02)	5.3 ±0.2[c] (0.43±0.02)
Incubating	19	..	14.6 ±0.9 (1.71±0.09)	...	3.9 ±0.2 (0.46±0.02)	...
Adults						
Molting	34	17	13.3 ±0.4 (1.64±0.04)	17.3 ±0.6 (1.53±0.05)	4.2 ±0.1 (0.51±0.01)	5.5 ±0.3 (0.48±0.02)
Fall	28	8	16.6 ±0.6 (1.83±0.06)	22.7 ±1.6 (1.74±0.13)	5.1 ±0.2 (0.56±0.02)	6.9 ±0.5 (0.53±0.04)
Winter	28	..	16.6 ±0.9 (1.72±0.07)	...	4.1 ±0.2[a] (0.44±0.02)	...
Prebreeding	16	..	21.8 ±1.0 (1.92±0.08)	...	4.8 ±0.2 (0.42±0.01)	...
Breeding	17	..	22.5 ±0.8 (2.02±0.07)	...	5.5 ±0.2 (0.49±0.2)	...
Incubating	10	..	13.1 ±0.6 (1.49±0.06)	...	4.0 ±0.2 (0.45±0.03)	...

[a] n=18. [b] n=29. [c] n=14.

cocks was during the breeding period. Ljunggren (1968:469) has reported similar findings for the wood pigeon (*Columba palumbus*) in Sweden. The pronounced decreases in the mean liver weights of hens from the breeding to the incubating period (38 percent for juvenile hens and 42 percent for adult hens) is indicative of the differences in circulating nutrient levels during the two periods. Livers were lightest, on the average, in adult hens collected during the incubating period and in adult cocks collected during the molting period.

The heart and lungs exhibited weight changes similar to those of the entire body (Table 13). The mean weights of hearts, relative to body weight, ranged from 0.36 to 0.46 percent among hens and 0.43–0.65 percent among cocks. The relative mean

Table 13.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of the heart and lungs from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Heart*		*Lungs*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	1.3 ±0.1 (0.40±0.01)	1.5 ±0.1 (0.43±0.01)	1.7 ±0.2 (0.51±0.03)	1.9 ±0.2 (0.55±0.03)
Fall	33	12	3.6 ±0.1 (0.42±0.01)	5.7 ±0.2 (0.49±0.01)	3.5 ±0.1 (0.41±0.01)	5.9 ±0.1 (0.51±0.01)
Winter	29	5	4.0 ±0.1[a] (0.46±0.01)	6.2 ±0.2 (0.53±0.02)	3.5 ±0.1 (0.40±0.01)	6.0 ±0.1 (0.52±0.01)
Prebreeding	14	13	4.3 ±0.2 (0.44±0.01)	8.5 ±0.2 (0.65±0.01)	4.7 ±0.4 (0.48±0.03)	7.5 ±0.3[d] (0.57±0.02)
Breeding	30	17	3.8 ±0.1 (0.37±0.01)	7.5 ±0.2 (0.61±0.02)	4.8 ±0.2[c] (0.46±0.02)	7.2 ±0.2[e] (0.57±0.02)
Incubating	18	..	3.4 ±0.1 (0.39±0.01)	...	3.7 ±0.2 (0.43±0.02)	...
Adults						
Molting	34	17	2.9 ±0.1 (0.36±0.01)	5.7 ±0.2 (0.50±0.01)	3.6 ±0.1 (0.44±0.01)	5.9 ±0.3 (0.52±0.02)
Fall	28	8	3.8 ±0.1 (0.42±0.01)	6.5 ±0.2 (0.50±0.02)	3.7 ±0.1 (0.41±0.01)	6.2 ±0.3 (0.48±0.03)
Winter	28	..	3.8 ±0.1[b] (0.41±0.01)	...	3.8 ±0.1 (0.39±0.01)	...
Prebreeding	16	..	4.5 ±0.1 (0.40±0.01)	...	4.8 ±0.2 (0.42±0.02)	...
Breeding	17	..	4.0 ±0.1 (0.36±0.01)	...	4.8 ±0.3 (0.43±0.02)	...
Incubating	10	..	3.7 ±0.2 (0.42±0.02)	...	3.6 ±0.1 (0.41±0.01)	...

[a] n=19 [b] n=18. [c] n=29. [d] n=12. [e] n=14.

weights of lungs ranged from 0.39 to 0.51 percent among hens and 0.48–0.57 percent among cocks. Several investigators have pointed out that heart weight is closely correlated with body weight in birds (see Hanson 1962*b*:59).

Changes in the mean weights or lengths of organs associated with the gastrointestinal tract (Tables 14–16) indicated that digestive activity was at its annual high in juvenile hens and adult hens during the breeding period and in juvenile cocks during the fall period. The mean weights of the gizzard and pancreas, and the mean lengths of the intestine, ceca, and colon of juvenile cocks were at their maxima during the fall period. Similarly, the mean weight of the pancreas, and the mean lengths of the intestine, ceca, and colon of hens were greater during the breeding period than they were during other periods in the annual cycle. The failure of the gizzard to increase in mean weight during the breeding period may be due, at least in part, to an increase in the availability of soft foods, such as insects, earthworms, and water-softened seeds. Kirkpatrick (1944: 185) reported that the mean weights of the organs of the digestive system in both juvenile hens and juvenile cocks were greatest in captive pheasants at the time of the most rapid body growth (14–19 weeks of age), which occurs during the early fall.

In my study, the gizzard and pancreas of juvenile hens (excluding growing hens) and of adult hens declined to their lowest mean weights during the incubating period (Tables 14 and 15). In cocks (excluding growing cocks), the mean weights of these organs were at their annual lows during the prebreeding period and winter period, respec-

Table 14.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of the spleen and pancreas from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Spleen*		*Pancreas*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	0.22±0.02 (0.07±0.01)	0.28±0.03 (0.08±0.01)	0.79±0.08 (0.24±0.01)	0.84±0.09 (0.24±0.02)
Fall	33	12	0.30±0.03 (0.04±0.00)	0.53±0.06 (0.04±0.00)	1.46±0.05 (0.17±0.01)	1.74±0.13 (0.15±0.01)
Winter	19	5	0.22±0.02 (0.03±0.00)	0.28±0.03 (0.02±0.00)	1.18±0.05 (0.14±0.01)	1.21±0.05 (0.10±0.00)
Prebreeding	14	13	0.36±0.02 (0.04±0.00)	0.37±0.04 (0.03±0.00)	1.44±0.08 (0.15±0.01)	1.35±0.08[d] (0.10±0.01)
Breeding	30	17	0.44±0.02 (0.04±0.00)	0.48±0.03[b] (0.04±0.00)	1.54±0.06 (0.15±0.01)	1.65±0.06 (0.13±0.01)
Incubating	19	..	0.33±0.02 (0.04±0.00)	...	0.89±0.06 (0.10±0.01)	...
Adults						
Molting	34	17	0.40±0.02 (0.05±0.00)	0.62±0.04 (0.05±0.00)	1.31±0.05 (0.16±0.01)	1.61±0.06 (0.14±0.00)
Fall	28	8	0.31±0.03 (0.03±0.00)	0.47±0.04[c] (0.04±0.00)	1.41±0.10 (0.15±0.01)	1.98±0.27 (0.15±0.02)
Winter	18	..	0.27±0.04 (0.03±0.00)	...	1.18±0.07 (0.13±0.01)	...
Prebreeding	16	..	0.37±0.04 (0.03±0.00)	...	1.28±0.09 (0.11±0.01)	...
Breeding	17	..	0.36±0.02 (0.03±0.00)	...	1.41±0.09 (0.13±0.01)	...
Incubating	10	..	0.30±0.03[a] (0.03±0.00)	...	0.98±0.07 (0.11±0.01)	...

[a] n=9. [b] n=16. [c] n=7. [d] n=12

Table 15.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of the gizzard and mean lengths, in centimeters, of the intestine from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Gizzard*		*Intestine*[a]	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	10.0 ±0.9 (3.11±0.13)	11.5 ±1.0 (3.33±0.15)	80.2±2.7	84.0±3.2
Fall	33	12	16.7 ±0.4 (1.98±0.04)	20.5 ±1.0 (1.74±0.09)	93.6±1.4[c]	105.2±1.9
Winter	19	5	14.5 ±0.4 (1.68±0.04)	16.4 ±0.3 (1.41±0.05)	85.3±1.7	91.5±3.4
Prebreeding	14	13	14.9 ±0.6[b] (1.55±0.04)	15.2 ±0.3 (1.16±0.04)	100.0±3.6[d]	94.4±3.1[e]
Breeding	30	17	16.0 ±0.4 (1.54±0.04)	16.3 ±0.5 (1.32±0.04)	108.5±2.0[e]	99.3±3.4
Incubating	19	..	13.4 ±0.4 (1.57±0.04)	...	88.5±2.8[f]	...
Adults						
Molting	34	17	17.5 ±0.6 (2.17±0.07)	18.5 ±0.8 (1.64±0.08)	95.5±1.9[g]	100.7±2.7
Fall	28	8	16.1 ±0.4 (1.77±0.04)	18.6 ±1.1 (1.43±0.08)	91.0±2.4[h]	102.0±4.5
Winter	18	..	13.9 ±0.4 (1.48±0.03)	...	84.2±1.7	...
Prebreeding	16	..	16.6 ±0.8 (1.47±0.07)	...	99.2±4.0[i]	...
Breeding	17	..	14.7 ±0.4 (1.32±0.03)	...	115.7±3.6[j]	...
Incubating	10	..	13.4 ±0.4 (1.54±0.06)	...	84.6±3.0[k]	...

[a] From pheasants collected in 1966, 1967, and 1968 only.

[b] n=13. [c] n=23. [d] n=4. [e] n=12. [f] n=16. [g] n=24. [h] n=18. [i] n=6. [j] n=10. [k] n=7.

tively. The intestine, ceca, and colon in all sex-age groups (disregarding juveniles during the growth period) were at their shortest mean lengths during the winter.

The testes of cocks increased in mean weight earlier and apparently remained heavy longer than did the ovaries of hens (Table 17). During the prebreeding period, testes were 75 percent of maximum mean weight, but ovaries had achieved only 2 percent (in juvenile hens) and 10 percent (in adult hens) of full development. Testes also increased in mean weight earlier than did ovaries in captive pheasants (Kirkpatrick 1944:182). Kirkpatrick, while conducting his study at Lafay-

Table 16.—Mean lengths and standard errors, in centimeters, of the cecum and colon from pheasants collected in east-central Illinois, 1966 through 1968.

Age and Period	*Sample Size*		*Cecum*		*Colon*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	14.4±0.6	14.9±0.7	7.0±0.3	7.1±0.3
Fall	23	12	18.0±0.5	20.5±0.6	8.9±0.1	9.8±0.2
Winter	19	5	16.0±0.4	18.5±1.6	8.7±0.1	9.4±0.3
Prebreeding	4	12	17.9±0.3	18.9±0.8	10.1±0.3	9.5±0.2
Breeding	12	17	19.5±0.8	19.3±0.9	10.5±0.3	9.6±0.2
Incubating	16	..	17.0±0.6	...	9.8±0.3	...
Adults						
Molting	24	17	16.4±0.5	17.5±0.5	9.9±0.2	9.6±0.2
Fall	18	8	15.4±0.4	18.6±1.5	9.3±0.2	9.6±0.2
Winter	18	..	15.4±0.5	...	9.2±0.2	...
Prebreeding	6	..	17.7±1.7	...	10.3±0.5	...
Breeding	10	..	19.7±0.9	...	10.6±0.4	...
Incubating	7	..	16.1±0.9	...	10.4±0.3	...

ette, Ind., found motile sperm in the testes, epididymides, and vasa deferentia as early as February 16. Hiatt & Fisher (1947:543) concluded that, in wild populations in Montana, cocks preceded hens by approximately 1 month in attaining complete gametogenesis. The advantages of cocks being in breeding condition for a longer period than are hens are self-evident.

The mean weights of the parathyroid glands were greatest in juvenile hens during the breeding period and in adult hens and juvenile cocks during the fall period (Table 18). Curiously, the parathyroids of adult hens weighed the least, on the average, during the breeding period. The main function of the parathyroid hormone is the regulation of ionized calcium in the extracellular fluid (Sturkie 1965:652; Ganong 1965:314). The circulating level of calcium acts directly on the parathyroid glands in a feedback fashion to control secretion of the hormone (Ganong 1965:320). When the calcium level is low, parathyroid hormone secretion is increased, and calcium is mobilized from the bones. Bloom, Nalbandov, & Bloom (1960:207) found that the parathyroids of laying chickens were twice as heavy in birds fed a low-calcium diet as they were in birds fed adequate amounts of this element.

The parathyroid glands of pheasants respond similarly to inadequate calcium intake; juvenile hens fed a low-calcium diet (corn only) for 8 weeks beginning October 20, 1966, had parathyroids that weighed an average of 9.9 ± 1.5 mg, whereas those of control birds averaged 4.1 ± 0.9 mg (R.F. Labisky & W.L. Anderson, unpublished data). In view of these findings, it seems strange that the mean weights —and presumably the activity—of the parathyroids of adult hen pheasants were greatly reduced during the breeding period. Obviously, the calcuim requirements of hens would be at a peak when the birds were laying. It is possible that adult hens obtain all the calcium they need for egg production directly from their diets. Hen pheasants increase their calcium intake by consuming calcium-rich grit during the breeding period (Harper 1964:266; Korschgen 1964:175–176; and Kopischke & Nelson 1966:273). The heavy mean weight of parathyroids found in adult hens during the fall indicates that these birds might be in a negative calcium balance.

Although there is disagreement regarding the proper interpretation of thyroid weights—i.e., their relation to thyroid activity—Kendeigh & Wallin (1966:377) stated that within any pas-

Table 17.—Mean weights and standard errors, in grams and as percentages of body weight (in parentheses), of the ovary, oviduct, and testes from pheasants collected in east-central Illinois, 1966 through 1969.

Age and Period	*Sample Size*		*Ovary*	*Oviduct*	*Testes*
	Hens	Cocks			
Juveniles					
Growth	16	17	0.04±0.01 (0.01±0.00)	0.04±0.01[b] (0.01±0.00)	0.02±0.00 (0.01±0.00)
Fall	33	12	0.09±0.00 (0.01±0.00)	0.10±0.00 (0.01±0.00)	0.20±0.01 (0.02±0.00)
Winter	19	5	0.12±0.01 (0.01±0.00)	0.12±0.01 (0.01±0.00)	0.28±0.04 (0.02±0.00)
Prebreeding	14	13	0.5 ±0.1 (0.05±0.01)	2.4 ±0.5 (0.24±0.05)	8.0 ±0.4 (0.61±0.03)
Breeding	30	13	26.9 ±1.5[a] (2.58±0.14)	22.3 ±0.7 (2.15±0.06)	10.6 ±0.5 (0.86±0.05)
Incubating	19	..	3.3 ±0.8 (0.36±0.08)	5.3 ±0.9 (0.60±0.09)	...
Adults					
Molting	34	17	0.46±0.04 (0.06±0.00)	0.82±0.06 (0.10±0.01)	2.71±0.38 (0.24±0.03)
Fall	28	8	0.26±0.02 (0.03±0.00)	0.46±0.02 (0.05±0.00)	0.26±0.02 (0.02±0.00)
Winter	18	..	0.24±0.02 (0.03±0.00)	0.49±0.03 (0.05±0.00)	...
Prebreeding	16	..	2.7 ±1.3 (0.24±0.12)	6.7 ±1.1 (0.59±0.10)	...
Breeding	17	..	28.3 ±1.6 (2.53±0.12)	22.5 ±0.6 (2.03±0.06)	...
Incubating	10	..	1.9 ±0.3 (0.21±0.03)	3.5 ±0.5 (0.39±0.04)	...

[a] n=29 [b] n=14

serine species the weight and volume of the thyroids are useful indices of thyroid activity, and that size is inversely correlated with activity. Harclerode & Dropp (1966:385), who worked with three species of pheasants, also found an inverse relationship between the weight and activity of the thyroids. However, both teams of workers believed that thyroid weight as an indicator of thyroid activity should be employed with caution.

The thyroid glands of pheasants and passerine birds apparently decrease in weight (increase in activity) during the colder months and increase in weight (decrease in activity) in the warmer months (Harclerode & Dropp 1966: 385; Kendeigh & Wallin 1966:376). Raitt (1968:368) reported that the thyroids in Gambel's quail (*Lophortyx gambelii*) were most active during June and December. After studying several reviews of the literature on the avian thyroid, Raitt (1968:370) concluded that thyroid activity was likely to be

Table 18.—Mean weights and standard errors, in milligrams and as percentages of body weight (in parentheses), of the parathyroids and thyroids from pheasants collected in east-central Illinois, 1967 through 1969. The percentage values (in parentheses) have been multiplied by 10^4.

Age and Period	*Sample Size*		*Parathyroids*		*Thyroids*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	11	9	2.2±0.6 (7.0±1.7)	2.2±0.5 (5.9±1.4)	17.7±1.9 (56.5±4.1)	20.3±1.8 (55.5±4.0)
Fall	24	9	5.9±0.7 (7.3±0.9)	6.3±0.7 (5.4±0.7)	42.2±3.3 (50.2±3.9)	58.0±5.2 (49.3±4.2)
Winter	26	5	5.1±0.5 (5.9±0.7)	5.1±0.9 (4.4±0.9)	35.0±2.5 (40.7±3.0)	31.8±3.7 (27.3±3.4)
Prebreeding	14	10	5.3±0.6 (5.6±0.7)	6.1±0.8 (4.7±0.7)	33.6±3.2 (34.5±2.9)	50.8±5.8 (38.7±4.5)
Breeding	29	11	7.7±0.7 (7.5±0.7)	5.6±0.8 (4.6±0.7)	48.9±2.6 (47.3±2.5)	45.8±3.4 (37.0±3.1)
Incubating	19	..	6.0±0.7 (7.1±0.8)	...	41.7±3.1 (48.7±3.3)	...
Adults						
Molting	27	13	6.4±0.6 (8.1±0.7)	5.9±0.6 (5.2±0.6)	47.2±2.2 (58.1±2.7)	51.2±3.2 (45.4±2.9)
Fall	22	8	8.3±0.8 (9.1±0.9)	9.7±1.2 (7.4±1.0)	45.1±2.3 (49.3±2.4)	61.7±5.1 (47.6±4.4)
Winter	24	..	6.3±0.5 (6.6±0.5)	...	41.9±3.3 (43.1±3.2)	...
Prebreeding	16	..	7.7±0.9 (6.9±0.9)	...	48.5±4.1 (43.1±4.1)	...
Breeding	17	..	4.5±0.6 (4.0±0.6)	...	43.0±3.5 (38.8±3.2)	...
Incubating	10	..	7.0±1.1 (7.9±1.3)	...	49.8±4.8 (56.7±5.3)	...

high in winter and in the period preceding the molt. In my study, the thyroid glands of all sex-age groups of pheasants were at or near their lowest mean weights during winter (Table 18), indicating high thyroid activity. The mean weights of thyroids were greatest in juvenile hens during the breeding period, in adult hens during the incubating period, and in juvenile cocks during the fall. Thyroids tended to be heavier, on the average, during the warmer periods (breeding, incubating, and molting) than during the fall and winter. Thus, seasonal changes in the mean thyroid weights—and presumably in thyroid activity—of pheasants in Illinois are generally similar to those of other avian species in temperate latitudes.

The adrenal glands of juvenile hens and adult hens were heavier, on the average, during the breeding, incubating, and molting periods than they were during the winter and prebreeding periods (Table 19). Among juvenile cocks, the mean weights of the adrenals were much greater during the prebreeding period than during any other time of the year. Kirkpatrick (1944:189) reported similar findings for captive pheasants. The increase in the mean adrenal weight in cocks coincides with the development of the testes (Table 17) and the beginning of breeding activities. Cock pheasants in east-central Illinois establish territories during March (S. L. Etter, Illinois Natural History Survey, Urbana, personal communication), or 2–4 weeks earlier than the period I have designated as the prebreeding period. Nagra, Breitenbach, & Meyer (1965:743) attributed this increase in the mean adrenal weight in cocks to the elevated secretion of ACTH arising from the inhibition of the negative feedback system by androgen. If the weight of the adrenals is a reliable indicator of stress, cock pheasants were subjected to considerable stress during the prebreeding period, but the duration of the stress was relatively short. The stresses imposed on hens, on the other hand, were apparently of lesser magnitude but persisted throughout the summer months.

Table 19.—Mean weights and standard errors, in milligrams and as percentages of body weight (in parentheses), of the adrenals from pheasants collected in east-central Illinois, 1967 through 1969. The percentage values (in parentheses) have been multiplied by 10^4.

Age and Period	*Sample Size*		*Adrenals*	
	Hens	Cocks	Hens	Cocks
Juveniles				
Growth	11	9	47.5± 3.9 (154.0±11.6)	45.1± 6.0 (128.3±17.5)
Fall	24	12	94.8± 3.1 (112.3± 3.9)	115.0± 6.0 (97.9± 5.2)
Winter	26	5	98.0± 4.0 (114.1± 5.4)	118.8± 4.9 (101.5± 4.6)
Prebreeding	14	10	87.0± 5.1 (90.2± 5.1)	154.7±13.0 (119.0±11.7)
Breeding	29	10	105.6± 4.3 (102.0± 4.5)	121.1± 8.1 (98.2± 8.3)
Incubating	19	..	108.0± 4.3 (127.3± 5.4)	...
Adults				
Molting	27	13	107.2± 3.4 (131.8± 4.0)	129.6± 7.0 (114.6± 5.5)
Fall	22	8	112.6± 4.6 (123.6± 5.0)	129.6± 8.2 (99.3± 5.8)
Winter	24	..	100.5± 6.0 (103.2± 4.9)	...
Prebreeding	16	..	103.4± 6.6 (90.9± 5.4)	...
Breeding	17	..	115.5± 7.2 (104.4± 7.0)	...
Incubating	10	..	106.2± 5.7 (121.4± 6.7)	...

The greatest mean weights of the thymus glands were recorded in juvenile pheasants during the growth and fall periods (Table 20). Thymuses in both juveniles and adults regressed markedly in mean weight from fall to winter and eventually descended to their annual low during the breeding

Table 20.—Mean weights and standard errors, in milligrams and as percentages of body weight (in parentheses), of the thymuses and bursa from pheasants collected in east-central Illinois, 1966 through 1968. The percentage values (in parentheses) have been multiplied by 10^4. Portions of the data for thymuses were reported in Anderson (1970).

Age and Period	*Sample Size*		*Thymuses*		*Bursa*	
	Hens	Cocks	Hens	Cocks	Hens	Cocks
Juveniles						
Growth	16	17	994± 143 (2,782± 212)	854± 79 (2,486± 134)	692± 79[b,c] (2,199± 157)	973± 65[b,f] (2,687± 182)
Fall	23	12	989± 93 (1,156± 104)	1,411± 159 (1,202± 137)	595± 61[b,d] (689± 69)	783± 82[b,g] (675± 73)
Winter	18	5	204± 36 (237± 43)	313± 26 (267± 20)	88± 11[b,e] (101± 12)	125± 44[b] (109± 39)
Prebreeding	4	12	257± 97[a] (282± 101)	128± 26 (99± 20)	. . .	. . .
Breeding	12	17	44± 18[b] (44± 18)	83± 21 (67± 17)	. . .	. . .
Incubating	16	. .	96± 35[b] (111± 40)	. . .	. . .	. . .
Adults						
Molting	24	17	821± 87 (1,007± 101)	964± 77 (856± 68)	. . .	. . .
Fall	18	7	513± 79 (556± 78)	481± 102 (366± 74)	. . .	. . .
Winter	18	. .	33± 12 (35± 13)	. . .	. . .	. . .
Prebreeding	5	. .	159± 49[a] (145± 46)	. . .	. . .	. . .
Breeding	10	. .	2± 1[b] (2± 1)	. . .	. . .	. . .
Incubating	7	. .	13± 7[b] (15± 8)	. . .	. . .	. . .

[a] From pheasants collected in 1968 only.

[b] From pheasants collected in 1967 and 1968 only.

[c] n=11. [d] n=14. [e] n=15. [f] n=9. [g] n=10.

period. However, when adult pheasants (former juveniles and "old" adults combined) began molting their primary flight feathers, their thymuses increased in mean weight once again. These seasonal changes, and the relationships between thymus weight increase and subsequent decrease and the progression of the molt of the primaries, are discussed in detail in another publication (Anderson 1970).

DISCUSSION

The underlying theme of much of this report is that heavy—and usually fat—pheasants are in good physical condition, and that light—and relatively fat free—birds are in comparatively poor condition. Although in the main this inference is probably correct, it does not hold true for all birds. A fat bird can be in poor condition. Indeed, chicks deficient in the essential amino acids methionine or lysine tend to be fat (Whittow 1965:261). Conversely, a bird that contains little fat can be in good condition. Whether a pheasant, fat or thin, is in good or poor condition is dictated to some extent by environmental factors. For instance, an accumulation of body fat probably helps wintering pheasants to tolerate low temperatures. At the other extreme, it might be advantageous for pheasants to be thin during the warmer months—when they are molting and are generally considered to be in poor condition.

Pheasants, like all other vertebrates, oxidize carbohydrates, fats, and proteins, the result of which is primarily the production of carbon dioxide, water, and the energy necessary for life processes. In birds, excess metabolic fuels are, for the most part, converted to fat for permanent storage (Whittow 1965:260). Protein, as such, cannot be permanently stored; Fisher (1954:45) stated that "deposit protein" is not a specialized storage product but the cytoplasm itself. Nevertheless, it is recognized that body proteins are a dynamic source of amino acids (Allison 1959:98).

Hanson (1962*a*:38–39) has emphasized that, under conditions of carbohydrate depletion, efficient metabolism of fat deposits necessitates simultaneous degradation of body proteins. Proteins and carbohydrates, upon being degraded, produce several compounds, one of which is oxaloacetic acid. This four-carbon acid must be present to condense with acetyl-Co A, a two-carbon fragment resulting from the reduction of fatty acids, before the metabolism of fats can proceed through the citric acid cycle. Ganong (1965:240) stated, "The main cause of relative or absolute impairment of the entrance of acetyl-Co A into the citric acid cycle is 'intracellular carbohydrate starvation.' When insufficient glucose is metabolized to pyruvic acid, the supply of oxaloacetic acid to condense with acetyl-Co A is inadequate *relative to the supply of acetyl-Co A* and the citric acid cycle cannot metabolize all of it" (emphasis added). Contrary to superficial appearances, this concept does not negate the more general belief that the starving animal *preferentially* metabolizes its glycogen reserves first, then its fat reserves, and finally its own body tissues. For a more detailed discussion of intermediary metabolism in relation to the energy demands of free-living birds, the reader is referred to Hanson's (1962*a*:33–40) treatise on the subject.

Exhaustion of carbohydrate reserves might be expected to occur during periods of starvation or fasting or when the diet is predominantly fat. Domestic chickens deplete their carbohydrate reserves in approximately 36 hours (range 24–48 hours) when food is not available (Benedict, Landauer, & Fox 1932:56–58).

Hormones have many, often complicated and poorly understood, influences on metabolic reserves. The pituitary, upon being stimulated by an increase in the photoperiod, releases gonadotrophins (Sturkie 1965:556), which bring birds into breeding condition. Estrogens secreted by the enlarged ovary promote increases in caloric intake and deposition of fat (Sturkie 1965:584). These increases were evident in pheasants during the prebreeding and breeding periods, when hens were fatter than cocks and adult hens were fatter than juvenile hens (Tables 5 and 6). Androgens have an anabolic action on muscular tissue (Russell & Wilhelmi 1960:146), which explains, at least partially, why the sternal muscles of cock pheasants did not decrease in mean weight as much as, and recovered more rapidly than, the sternal muscles of hen pheasants during the spring and summer months (Table 3). Hanson (1962*a*:32), while discussing relationships between metabolic reserves and hormones in Canada geese, stated, "it appears that the gonadal hormones confer on each sex a distinctive metabolic advantage in terms of survival: the males, because of greater initial protein stores and the nitrogen-conserving influence of the androgens, apparently undergo the moult with less ill effect than the females; the latter, on the other hand, can probably more readily survive most times of starvation stress because of superior fat reserves —the result of the influence of estrogens and, presumably, a lower metabolic rate."

According to Russell & Wilhelmi (1960:175–176), it is well established that adrenocortical hormones promote catabolism of body proteins. Masoro (1966:74) reported that these hormones have similar effects on adipose tissue. However, White (1956:141) asserted that the adrenocorticoids can be either anabolic or catabolic on protein metabolism. Harris (1970:753) has proposed that the adrenocorticoids are instrumental in mobilizing "tissue reserves" to meet energy demands in laying and incubating blue-winged teal. In my study, the adrenals of pheasants became enlarged in cocks during the prebreeding period and in hens during the breeding period (Table 19). These periods correspond with the early stages of the downward trends in condition parameters of the respective sexes (Fig. 2).

Russell & Wilhelmi (1960:187) stated that, "The relationship of the thyroid hormone to protein metabolism is biphasic. On the one hand, . . . small amounts of thyroxine are necessary for normal growth and development, so that in this sense the hormone is anabolic. On the other hand, the 'basal' rate of protein catabolism is correlated directly with the basal metabolic rate." Thyroxine is one of several factors that influence the molt in birds, but its exact role is not understood (Ringer 1965:624–625). Insulin appears to have a conserving effect on amino acids (Russell & Wilhelmi 1960:158).

It appears that pheasants wintering in east-central Illinois experience little difficulty in fulfilling their energy requirements. The body weights of pheasants, at least of hens, were relatively constant during the four winters included in this study (Table 2). Furthermore, body weights remained stable or increased slightly from fall to winter and increased appreciably from winter to the prebreeding period (Fig. 2). The failure to find birds in poor physical condition during the winter months was not surprising, as stresses on pheasants wintering in east-central Illinois do not appear to be severe. Food, primarily waste corn and soybeans, is abundant, and winter storms are relatively mild compared with those characteristic of more northern and western portions of the continental pheasant range. Pheasants rarely die as a direct result of winter storms in Illinois.

The pronounced increases in mean body weight from the winter to the prebreeding period, achieved primarily by deposition of fat, presumably represent increases in reserves of metabolic fuels accumulated in preparation for the stresses of breeding and nesting activities. Increases in the mean weight of the gizzard and in the mean lengths of the intestine, ceca, and colon of hens from the winter to the prebreeding period (Tables 15 and 16) suggest that food consumption and digestive activity increase during the latter period. While conducting an experiment with captive pheasants, Breitenbach et al. (1963:27) found that food consumption increased 39 percent from February to April. However, because pheasants on limited food intake were also capable of increasing the weights of their gastrointestinal tracts (Breitenbach et al. 1963:29), factors other than food consumption must contribute to the enlargement of the gizzard and intestinal mass.

As might be expected, my findings indicate that cock pheasants are in an extreme state of physiological and behavioral stress during the prebreeding period—i.e., the period of territory establishment. The mean weights of their legs, hearts, and lungs were increased appreciably—implying increased physical activity; their testes had reached 75 percent of full development—implying elevated androgen levels; and their adrenals were at maximum annual size—implying a state of stress (Tables 3, 13, 17, and 19). None of these physiological manifestations were particularly evident in hens during the prebreeding period.

Findings of this study illustrate beyond a reasonable doubt that hen pheasants mobilize appreciable quantities of muscular tissue and fat during the breeding and incubating periods. The mean weights of the fat strip and visceral fat of juvenile hens and adult hens decreased more than 90 percent from the prebreeding period to the molting period (Fig. 2). Similarly, the sternal muscles of juvenile hens and of adult hens decreased, on the average, 18 and 25 percent, respectively, during the same time.

The significant inverse relationships between the weights of muscular tissues and the advancement of the collection date for breeding hens, and the lack of such relationships for incubating hens (Fig. 3 and 5), probably are reflections of the high protein requirements of egg production. As was pointed out earlier, the mean weights of the sternal muscles of hens steadily decreased from the prebreeding period through the breeding and incubating periods and into the molting period. However, when the mean weights of sternal muscles were plotted as percentages of body weights, notable increases in the relative weights of these muscles occurred between the breeding and incubating periods (Fig. 2). The weights of fat deposits, on the other hand, exhibited significant inverse relationships with the progression of the collection date for both breeding hens and incubating hens (Fig. 3 and 5). Fat deposits steadily decreased both in actual weight and in relation to body weight between the prebreeding period and the molting period (Fig. 2). Therefore, it seems plausible that muscular tissue was mobilized comparatively rapidly during the breeding (laying) period and comparatively slowly during the incubating period.

It has been shown in this study (Fig. 2), as well as in those by Kirkpatrick (1944:180) and Kabat et al. (1956:5), that metabolic reserves of pheasants are at, or near, annual lows during the molting period. Kabat et al. (1956:13) demonstrated that the ability of hens to survive applied stresses (caging and starvation) was at a minimum during this period; their experimental birds survived an estimated 13 days. Molting pheasants are light in weight primarily because they possess little body fat (Fig. 1 and 2).

However, this discussion is in no way intended to imply that the welfare of pheasants in Illinois is in jeopardy during the molting period. It is difficult to imagine that a fat (winter-type) pheasant would be better prepared than a thin (summer-type) pheasant to cope with the hot, humid conditions that are characteristic of east-central Illinois during July and August. Baldwin & Kendeigh (1938:456) stated, "heavier birds have a greater resistance than do lighter birds to low temperature over a period when obtaining food is difficult . . . . At high air temperatures the reverse is true. Lighter birds generally have a greater resistance to heat, since the proportion of their body surface area (internal and external) to body mass is greater, and surplus body heat may be dissipated more rapidly." In birds growing new feathers, heat loss may be enhanced by the presence of blood quills, which increase the surface through which blood flows (Breitenbach & Baskett 1967: 215).

While it is recognized that the molting of old feathers and the growth of new ones place physiological stresses on birds, the process is leisurely in pheasants. In fact, condition parameters of pheasants steadily increase in value as the molt progresses (Fig. 6). This leisurely molt is in sharp contrast with that of Canada geese, in which all primaries are lost simultaneously and body weight decreases as the new feathers increase in length (Hanson 1962*a*:13). The greatest demands on metabolic reserves in geese apparently occur during the molt, whereas in pheasants they occur during the breeding and, for hens, the incubating periods.

Errington (1939:35) found that captive pheasants reduced to 671 grams (75 percent of initial weight) by starvation were capable of recovering to 94 percent of their initial weight after being returned to "full feed" for 3 weeks. Of the pheasants examined during my study, the only ones, excluding chicks, that weighed less than 700 grams were two adult hens collected during the molting period. These birds weighed 659 and 679 grams, or 76 and 79 percent of the mean weight of juvenile hens in winter. The sternal muscles of these hens weighed 31 and 25 percent less than the mean weight of the sternal muscles of wintering juveniles. The sternal muscles of juvenile hens that had died of starvation weighed about 75 percent less, on the average, than those of winter juveniles (Table 8). Hanson (1962*a*:54–55) reported that the sternal muscles of adult Canada geese weighed 32–33 percent less during the nonflying stage of the molt than they weighed during the winter. I concluded, somewhat subjectively, that hen pheasants in east-central Illinois might be capable of reducing their body weight to 690 grams (80 percent of the mean weight of winter juveniles) and their sternal muscles to 175 grams (75 percent of the mean weight of the sternal muscles of winter juveniles) without seriously affecting their health and survival chances. These values, intended to apply only to hens actively molting, rarely occur among pheasants in Illinois.

The summer-to-fall increases in the mean body weight and the mean weights of muscular tissues and fat deposits of adult pheasants appeared to be of sufficient magnitude to restore metabolic reserves to levels similar to those of wintering juveniles (Tables 2–4). When fall-collected adult birds were compared with juveniles collected during the same period, the former appeared to be in better physical condition than were the juveniles (Table 6).

Juvenile pheasants would probably suffer more than would adults from inadequate food intake, which might occur in Illinois following an unusually severe snowstorm. The mean body weights of adult hens and adult cocks were 12 and 18 percent greater than those of juvenile hens and juvenile cocks during the winter (Table 2). Fat deposits were twice as large, on the average, in adult hens as they were in juvenile hens (Table 4). These differences were statistically significant ($P<0.05$).

The evidence also suggests that adult hens enter the breeding period in better physical condition than do juvenile hens (Tables 2–4 and 6). Thus, adult hens might be expected to perform better reproductively than juvenile hens. Data on the status of reproductive organs during the prebreeding period suggested that adult hens become sexually active at an earlier date than do juvenile hens (Table 17), and linear regressions implied that, for any given date during the breeding period, adults will have produced more eggs than juveniles will have produced (Fig. 3). Labisky & Jackson (1969:720), after studying the production and weights of eggs laid by captive pheasants, concluded that "2-year-old hens probably represent the most competent reproductive age-class in populations of wild pheasants." These investigators went on to state, "In east-central Illinois, adult hens constituted 44 ± 2 (SE) percent of the spring population of hen pheasants during the 6 years, 1957–62 (R. F. Labisky, unpublished data). Adult hens, of which 2-year-olds make up the overwhelming majority in spring, nest substantially earlier than most yearlings (Labisky 1968*b*:70, 77); not only the rate of success, but also the clutch size, of early-season nests exceeds those of late-season nests (Labisky 1968*b*:128, 186). Consequently, 2-year-old hens may contribute proportionally more young to the population annually than would be expected on the basis of their proportionate occurrence in the breeding flock."

Hanson (1962*a*:42) emphasized that, in the management of Canada geese, consideration should be given to the quality of foods made available to wintering birds. He specifically suggested that dwarf varieties of sunflowers, excellent sources of the sulfur amino acids methionine and cystine, be planted on refuges. While pheasants differ greatly from geese in numerous ways, the need for quality foods, particularly high-grade protein, is nearly universal among avian forms. Young pheasants and young bobwhite quail (*Colinus virginianus*), like young chickens, have high requirements for methionine plus cystine, needing approximately 3.5 grams of these amino acids per 100 grams of protein in a 26.5-percent protein diet (Scott, Holm, & Reynolds 1963:680).

Unlike the opportunities offered by wintering geese, opportunities to provide quality foods for pheasants are limited, at least in Illinois, because these birds are widely distributed over their range throughout the year and they occur primarily on private lands. However, where acreages are available, plant species that produce seeds containing large amounts of the sulfur amino acids could be planted to provide these nutrients. The methionine-rich, high-protein floury-2 mutant of corn (Nelson, Mertz, & Bates 1965: 1470) should be particularly valuable for this practice, since corn (*Zea mays*) is an important food for pheasants throughout much of their range. Federal, state, and local government holdings; private hunting preserves; and farmlands that have been removed from production might be used for such plantings. Roadsides might be suitable in some areas, provided low-growing plants are used. The amino acid compositions of the seeds of a large number of plant species have been determined by VanEtten et al. (1961, 1963, 1967) and Miller et al. (1962*a*, 1962*b*).

Winter feeding programs intended to provide food for large flocks of pheasants might be practical in some instances, especially if emphasis is placed on the quality of the foods that are distributed. However, because carbohydrates have a conserving effect on body protein, a food low in proteins but high in sugars and starches would obviously contribute more to the welfare of these birds than merely serving as a source of calories. The importance of an adequate diet for pheasants during late winter is underscored by Gates & Woehler's (1968:245) conclusion that low body weights during this period result in delayed egg laying and in accelerated mortality of adult hens during the summer.

SUMMARY

1.—This study involved collecting 363 pheasants (274 hens and 89 cocks) from wild populations in east-central Illinois, weighing them, and dissecting them to obtain, in addition to body weight, weights or measurements of muscular tissues, fat deposits, and internal organs. The pheasants were collected during designated periods (growth, fall, winter, prebreeding,

breeding, incubating, and molting) of the life cycle, 1966 through 1969. For the purposes of this study, all pheasants less than approximately 13 months of age—i.e., pheasants that had not entered into their first postnuptial molt—were considered *juveniles*, and all other birds were considered *adults*.

2.—The mean relative weights (i.e., relative to body weight) of muscular tissues (sternal muscles and legs) and of fat deposits (fat strip and visceral fat) were similar between the sexes during the fall and winter periods. However, hens, when compared with cocks, had, on the average, relatively small sternal muscles during the breeding and molting periods and relatively small legs during the prebreeding and breeding periods. Hens were, on the average, much fatter than were cocks during the prebreeding and breeding periods.

3.—The mean weight of the entire bird and mean relative weights of the fat deposits were lower for juvenile hens than for adult hens during all periods except the incubating period. The mean relative weights of legs, however, were greater for juvenile hens than for adult hens during the fall, prebreeding, and breeding periods.

4.—Linear correlations indicated that the weights of sternal muscles, of legs, and of fat deposits were positively related to body weight. However, when expressed on a relative basis, the weights of sternal muscles and of legs tended to be inversely related to body weight, suggesting that the seasonal variations in body weight were determined primarily by variations in the amount of fat in pheasants.

5.—The mean body weights of juvenile hens, relative to their mean body weights during winter, were 112 percent during the prebreeding period, 120 percent during the breeding period, 99 percent during the incubating period, and 94 percent during the molting period. During the same periods, adult hens, compared with juvenile hens in winter, had mean relative body weights of 132, 129, 102, and 94 percent, respectively. The mean body weights of juvenile cocks, relative to the mean body weight of the wintering juvenile cock, were 112, 106, and 97 percent during the prebreeding, breeding, and molting periods, respectively.

6.—The mean body weight of adult hens and of adult cocks increased an average of 13 and 15 percent, respectively, between the molting and fall periods. These increases appeared to be sufficient to restore metabolic reserves to levels similar to those of wintering juveniles.

7.—Multiple regressions indicated that (i) negative relationships existed between body weight, or sternal muscles, or legs, or fat deposits and the independent variables—eggs laid and collection date—for breeding hens; (ii) negative relationships existed between fat deposits and the independent variables—days of incubating and collection date—for incubating hens; and (iii) positive relationships existed between body weight, or sternal muscles, or legs, or fat deposits and the independent variables—primary feathers molted and collection date—for molting hens and molting cocks. Further testing indicated that the second independent variable—collection date—contributed more to the regressions for breeding hens and incubating hens than the first independent variable—number of eggs laid and days of incubating, respectively.

8.—Mean relative weights of the heart and lungs were smaller, and those of the pancreas and gizzard larger, for hen pheasants than for cocks during most of the annual cycle.

9.—Juvenile pheasants, when compared with adults, had, on the average, relatively small reproductive organs during the fall and winter periods but relatively large gizzards and thymuses during most of the annual cycle. Juvenile hens also had, on the average, proportionately larger livers, pancreases, spleens, gizzards, parathyroids, and thyroids than adult hens had during the breeding period, apparently because adult hens are exceedingly heavy (fat) during this period. The mean weights of internal organs were proportionately greater among young growing pheasants than they were among older birds.

10.—Changes in the mean weights or measurements of organs associated with the gastrointestinal tract indicated that digestive activity was at its annual high in juvenile hens and adult hens during the breeding period and in juvenile cocks during the fall period. The mean weights of the gizzard and pancreas and the mean lengths of the intestine, ceca, and colon of juvenile cocks were at their maxima during the fall period. Similarly, the mean weight of the pancreas and the mean lengths of the intestine, ceca, and colon of hens were greater during the breeding period than during other periods in the annual cycle.

11.—Cock pheasants appeared to be in a state of extreme physiological and behavioral stress during the prebreeding period—i.e., the period of territory establishment. The mean weights of their legs, hearts, and lungs were increased appreciably—implying increased physical activity; their testes were at 75 percent of full development —implying elevated androgen levels; and their adrenals were at maximum annual size—implying a state of stress.

12.—Pheasants wintering in east-central Illinois apparently experience little difficulty in fulfilling their energy requirements. The mean body weights of hens were relatively constant during the four winters in which pheasants were collected for this investigation. Furthermore, mean body weights remained stable or increased slightly from fall to winter and increased appreciably from winter to the prebreeding period.

13.—Hen pheasants appeared to mobilize appreciable quantities of muscular tissue and fat during the breeding and incubating periods. The fat strip and visceral fat of juvenile hens and of adult hens decreased in mean weight by more than 90 percent from the prebreeding period to the molting period. Similarly, the mean weights of the sternal muscles of juvenile hens and of adult hens decreased an average of 18 and 25 percent, respectively, during the same time.

14.—The available evidence indicated that, among hens, muscular tissue shrinks at a faster rate than do fat deposits during the breeding period, while the reverse is true when the hens are incubating.

15.—It is suggested that molting hens in east-central Illinois might be capable of reducing their body weight to 690 grams (80 percent of the mean body weight of winter juveniles) and their sternal muscles to 175 grams (75 percent of the mean weight of those of winter juveniles) without seriously affecting their health and survival. These values, intended to apply only to hens actively molting, rarely occur among pheasants in Illinois.

16.—The results of this investigation suggest that whenever feeding programs are initiated for pheasants, priority should be given to plant species that are rich in the sulfur amino acids. The high-methionine floury-2 mutant of corn should be especially valuable for this purpose.

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